





THE VERTEBRATE FAUNA OF THE
SELMA FORMATION OF ALABAMA

PART IV
THE TURTLES OF THE FAMILY TOXOCHELYIDAE

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CURATOR OF FOSSIL REPTILES

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PREFACE

Turtles belonging to the family Toxochelyidae constitute by far the largest part of the material collected in the Mooreville Chalk of the Selma Formation. Not only is the number of specimens considerable, but the materials belong to a relatively large number of genera and species. This is true not only in the Mooreville Chalk, but likewise in the Niobrara Chalk of Kansas. The Toxochelyidae, rather than the Protostegidae, formed the most conspicuous elements of the turtle fauna.

The study of toxochelyid turtles is beset with a great many difficulties, paramount among which are the relatively poor state of preservation of most specimens and the fact that entire shells are very rare finds. Most specimens consist of only a very small portion of the skeleton and, more often than not, the remains are badly crushed and often distorted as well as flattened.

The question exists whether materials of this kind furnish enough evidence to permit significant conclusions as to the morphology of the original animals. The answer is, I believe, favorable in this case, because of the relatively large number of available specimens and because of the fact that the turtle skeleton generally conforms to a very rigid, basic pattern of organization. In a single family, such as the Toxochelyidae, this basic pattern of organization to which all of the genera conform is so stable that unknown parts can be predicted to a considerable extent on the basis of the known portions of the skeleton. This is especially true in the case of the shell, where the elements show the same fundamental relationships to one another in all species of the family. It is, for instance, not necessary to have all twenty-two peripheral plates in a given specimen in order to be certain that normal individuals of the species possessed that many; if only one mid-dorsal neural plate is preserved, and this is keeled, it is entirely safe to predict a carapace with a sagittal carina. Fragmentary specimens, if available in sufficiently large numbers, permit essentially accurate reconstruction of the shell.

The major difficulty in the study of the toxochelyid turtles is not so much the fragmentary state of the remains as the varying degree to which the materials are deformed. There is evidence among the materials from the Mooreville Chalk of Alabama that compression may have reduced shell plates to as little as 20 per cent of their original thickness. Crushing results in greater or lesser alterations in the shape of the bones, and these alterations present a major obstacle in the comparison of specimens. Familiarity with the materials can partially overcome this difficulty, but it is often impossible to distinguish individual variations in form from individual differences in preservation.

In view of the difficulties mentioned, the systematic treatment of the material must be conservative. It is possible that fewer species are here recognized than actually existed.

It was evident from the beginning that the toxochelyid materials from Alabama could not be satisfactorily studied by themselves. A review of all of the materials of toxochelyid turtles was inevitable and to this end I visited all major collections in the United States that preserve specimens of this group.

I wish to express my sincere gratitude to the authorities of the American Museum of Natural History, the United States National Museum, the Peabody Museum of Yale University, the Museum of Natural History of the University of Kansas, the Academy of Natural Sciences of Philadelphia, the Natural History Museum at South Dakota School of Mines, and the University of Tennessee for the privilege of studying their materials. I feel greatly indebted to my colleagues in charge of these collections for their kind help during my visits and for the loan of much of the important Niobrara material. I was thus enabled to assemble for direct comparison most of the toxochelyid materials known at present.

My very best thanks are due, furthermore, to Mr. C. M. Barber, of Flint, Michigan, who collected much of the Alabama material, and to Mr. William D. Turnbull, of Chicago Natural History Museum, who collected some of the specimens and took a great interest in the patient and skillful preparation of the entire Mooreville Chalk collection.

The drawings were made by the late John Conrad Hansen (figs. 61, 91, 100, 112 in part), Mr. Douglas E. Tibbitts (figs. 105, 117), Miss Maidi Wiebe (figs. 63, 70, 90, 122-124, pl. 20), and myself. The photographs were made by Mr. John Bayalis (pls. 10, *c*, 11-13, 17-19, 21-25) and myself. A number of photographs (pl. 15, figs. 3, 4, pl. 16, figs. 2-12) were kindly given to me by the American Museum of Natural History.

RAINER ZANGERL

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Turtles of the Family Toxochelyidae



INTRODUCTION

In his revision of the fossil turtles of North America, Hay (1908) included in the family Toxochelyidae only the genera *Toxochelys* Cope, *Porthochelys* Williston, and the little-known *Cynocercus* Cope. Several other forms were placed among the Thalassemyidae, namely, *Osteopygis* Cope, *Catapleura* Cope, *Lytoloma* Cope, *Erquelinnesia* Dollo, and *Rhetechelys* Hay.

Hay's reasons for placing the latter genera in the Old World family Thalassemyidae are not known; he characterized the family *after* having included the above genera in it. Apparently, morphological criteria were not the reason. There is a far greater degree of similarity between the skulls and mandibles of the genera in question and those of the cheloniid turtles than there is between any of these forms and the thalassemyids. Furthermore, there is a striking similarity between the plastra of *Osteopygis* and *Toxochelys* or *Porthochelys*. Thus, the morphological affinities of the four genera in question are with the Cheloniidae and the Toxochelyidae, not with the Thalassemyidae. As will be shown below, the basic organization of the Thalassemyidae is very different from that of any of the genera listed above.

I have come to the conclusion that there is a convergence in the development of secondary palates and wide mandibular triturating surfaces in the genera *Osteopygis* and *Rhetechelys* on the one hand and the cheloniid turtles on the other and that the forms mentioned belong to the family Toxochelyidae.

The materials referred to the genus *Lytoloma* from the Greensand deposits of New Jersey have long been a source of confusion. The type material on which the type species, *L. angusta* Cope, is based consists of some peripheral plates (A.M.N.H. 1133), one of which was figured by Cope,¹ as has been elaborately demonstrated by Hay (1908, p. 155, fig. 192). A mandible bearing the same catalogue number (A.M.N.H. 1133) was evidently not associated with the peripheral bone and was not used by Cope to establish either the genus or the species. The mandible bears a label in Cope's handwriting: "*?Lytoloma angusta* Cope, Birmingham, N. J." (see pl. 15, fig. 4). Hay argues correctly that Cope would hardly have doubted the identification of this specimen had he regarded it as part of his type material.

¹ There seems to be some doubt as to the association of these bones.

With the association of these bones in doubt, the one peripheral plate figured by Cope becomes the sole name-bearer. The latter is, however, not characteristic of any specific group of turtles. It might belong to a cheloniid, to *Osteopygis*, *Catapleura*, or *Toxochelys*. The mandible, poorly preserved, is indistinguishable from that of *Osteopygis*. In view of the fact that Cope did not make the mandible the name-bearer of the genus and species and since the peripheral is unidentifiable, I suggest that the name *Lytoloma angusta* be considered a nomen vanum. The mandible (A.M.N.H. 1133) is here referred to the genus *Osteopygis* and likewise a mandible (Y.P.M. 913) and an anterior skull fragment (Y.P.M. 913a) that had been referred to *Lytoloma angusta* by Wieland (1904b). This lower jaw (Y.P.M. 913) was made the type of Hay's *Lytoloma wielandi* (Hay, 1908), and the skull fragment was assigned to this species along with a fairly complete carapace (Y.P.M. 625). The latter is here recognized as a member of the genus *Toxochelys* and is designated as the type of *T. atlantica* sp. nov. (p. 196).

The unfigured type material, consisting of a questionable nuchal and a first peripheral, of *Lytoloma jeanesi* Cope is lost. The referred bones (A.M.N.H. 1473), figured by Hay (1908, p. 157, figs. 193-195), belong very probably to a mixed specimen. The first peripheral might belong to *Toxochelys* and the sixth peripheral to *Osteopygis*. *L. jeanesi* Cope must also be regarded as a nomen vanum.

The various species from the London Clay, referred to *Lytoloma* by Lydekker (1889), will have to be reassigned; but to do this from the literature would, I fear, merely result in a further complication of their already confused taxonomic status. A restudy of the European material seems necessary to determine the generic allocation of these species.

Until now, it was understood that the genus *Toxochelys* (even though some species were known from skulls only) included those members of the family Toxochelyidae whose carapaces have a strong sagittal carina extending from the first neural plate to the suprapygal area. This was a proper deduction, since none of the previously studied specimens that were associated with parts of the carapace lacked a mid-dorsal keel.

Recently, Chicago Natural History Museum received a partial skeleton, without skull, of a turtle from the Niobrara deposits of Kansas (C.N.H.M. PR123). The carapace differed from any known member of the genus *Toxochelys* by the absence of a carina, yet it could not be identified with *Porthochelys laticeps*, the only previously known flat-neuraled toxochelyid from the Niobrara. On the other hand, C.N.H.M. PR123 agreed very closely with the most common, unkeeled toxochelyid from the Mooreville Chalk of Alabama. The suspicion arose that the genus *Toxochelys* might include flat-neuraled as well as carinated forms, but this could not be proved until an unpublished, unkeeled specimen with the skull associated was discovered in the collection of Yale Peabody Museum (Y.P.M. 3602). The skull leaves no doubt as to the species to which this individual belongs—*Toxochelys latiremis* Cope, the type species. Thus, unfortunately, the familiar picture of the carinated chelonian from the Niobrara must

be divorced from the equally familiar name *Toxochelys*, which name now applies to a far less spectacular group of turtles.

The genus *Catapleura* Cope appears to be a primitive cheloniid that connects the families Cheloniidae and Toxochelyidae (see p. 267).

Phyllemys Schmidt belongs to *Toxochelys*. The isolated mandible from New Jersey on which Hay based his *Erquelinnesia molaria* (Hay, 1908) very probably belongs to *Osteopygis*. *Rhetechelys* Hay is tentatively included as an osteopygine toxochelyid, but it may possibly be a cheloniid.

The family Toxochelyidae includes, under the present interpretation, the following genera:

Carapace unkeeled: *Toxochelys* Cope, *Porthochelys* Williston, *Thinochelys* gen. nov., *Osteopygis* Cope.

Carapace keeled: *Lophochelys* gen. nov., *Ctenochelys* gen. nov., *Prionochelys* gen. nov.

Incertae sedis: *Cynocercus* Cope, *Rhetechelys* Hay.

As will be shown, our knowledge of the toxochelyid turtles has increased considerably since Hay's revision. In addition to the then known occurrences in the Niobrara Chalk of Kansas, the Pierre Shale of South Dakota, Wyoming, and Kansas, and the Greensand deposits of New Jersey, toxochelyid turtles have since been collected from the Mooreville Chalk of the Selma Formation of Alabama, the Taylor Marl of Texas, the Marlbrook Marl of Arkansas and the Coon Creek Tongue of the Ripley Formation of Tennessee. Furthermore, notable additional collections have accumulated from the Niobrara and the Pierre.

Abbreviations of Institutions

A.M.N.H. = American Museum of Natural History
A.N.S.P. = Academy of Natural Sciences of Philadelphia
C.N.H.M. = Chicago Natural History Museum

K.U. (V.P.) = University of Kansas Museum of Natural History
S.D.S.M. = South Dakota School of Mines
U.S.N.M. = United States National Museum
U.T. = University of Tennessee
Y.P.M. = Yale Peabody Museum

See figure 29, Part III of this volume, for the names of localities used in designations of the Alabama specimens.

GENERAL MORPHOLOGY OF THE TOXOCHELYIDAE

The Toxochelyidae are a group of marine turtles whose degree of aquatic specialization ranges from that of near-shore dwellers to that of very highly advanced, efficient sea-faring types. The outstanding aquatic specializations appear in the differentiation of the skull, the shell, and the forelimbs but are by no means typical for this family. Both carapace and plastron are relatively light in construction, and in nearly all of the forms fontanelles occur between the costal plates and the peripherals in the carapace, and central and lateral fontanelles

occur in the plastron. The more generalized representatives have an unkeeled shell of oblong, or, more commonly, circular outline, whereas the advanced species are provided with a mid-dorsal carina and the outline of the carapace tends to be cordiform.

Skull

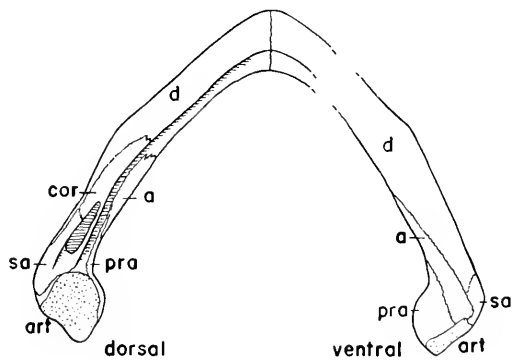
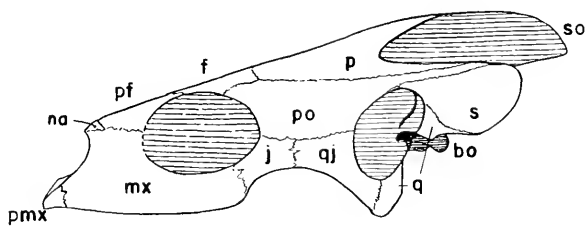
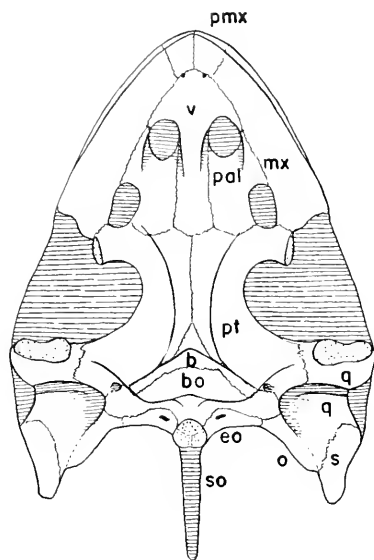
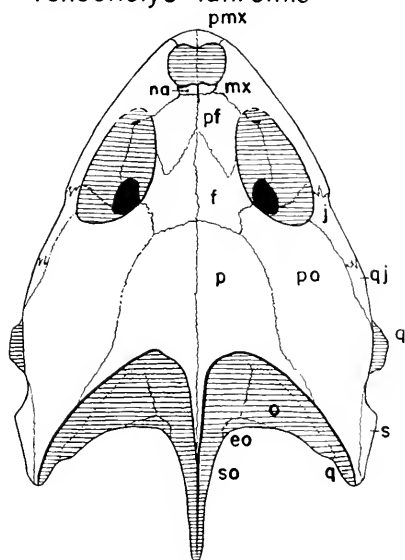
An unusually large number of toxochelyid skulls and skull fragments have accumulated in various collections. Most of the material belongs to *Toxochelys latiremis*, so that the following account is based primarily, though not exclusively, on this species. The vast majority of the skulls have been found isolated, but the few specimens associated with shell material have made possible the proper allocation of all skull and jaw specimens to species also known from shells. The state of preservation must be discussed here because it tends to bias the comparison with such Recent forms as sea turtles and snapping turtles. Quite generally, the skulls are crushed dorso-ventrally to a much greater extent than is apparent at casual examination. Taking a moderate amount of flattening into account, one is led to compare the over-all shape of the toxochelyid skull with that of the common snapping turtle (*Chelydra serpentina*). More careful analysis of the crushing and some rare, uncrushed fragments reveal, however, that the toxochelyid skull is much higher than the chelydrid skull, possibly as high as that of the Recent *Caretta*.

The toxochelyid skull is more or less triangular in dorsal outline, with broadly rounded sides and a fairly blunt snout region. Its height is difficult to determine, but it probably approximates that of the modern sea turtles; it is most certainly higher than the skull of *Chelydra*. The palate is a primary one, except in the Osteopyginae, which possess a solid secondary palate much as the Recent *Caretta*. The orbits face outward and upward and the external nasal opening faces forward and upward. The posterior excavation of the roof of the skull is intermediate in extent between that of living sea turtles and snapping turtles. Regarded as a whole, the toxochelyid skull combines features observed either in cheloniid or chelydrid turtles; only rarely are they intermediate between the compared conditions.

The general arrangement of the bones of the skull roof resembles that of Recent sea turtles. In the Toxochelyinae and Lophochelyinae, the frontals form part of the dorsal rims of the orbits (fig. 60); in the Osteopyginae (e.g. in *Rhetchelys*) the frontal bones do not reach the orbital rims. The postorbital bones extend much farther backward than in cheloniid or snapping turtles, namely, to the very tips of the squamosal processes. The squamosal bones are unusually

FIG. 60. Reconstruction of skull of *Toxochelys latiremis*. *a*, angular; *art*, articular; *b*, basisphenoid; *bo*, basioccipital; *cor*, coronoid; *d*, dentary; *eo*, exoccipital; *f*, frontal; *j*, jugular; *mx*, maxilla; *na*, nasal; *o*, opisthotic; *p*, parietal; *pal*, palatine; *pf*, prefrontal; *pmx*, premaxilla; *po*, postorbital; *pra*, preangular; *pt*, pterygoid; *q*, quadrate; *qj*, quadrato-jugal; *s*, squamosum; *sa*, surangular; *so*, supraoccipital; *v*, vomer.

Toxochelys latiremis



small, forming only the ventro-lateral (but not the dorsal or medial) faces of the squamosal processes (fig. 60). The squamosals are thus excluded from contact with the parietal bones, a condition not due merely to the posterior excavation of the skull roof, as in the snapping turtles and many other forms. Small nasal bones have definitely been observed in *Toxochelys* and *Porthochelys*.

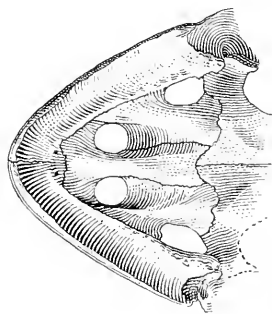
The bones of the ventral and posterior faces of the skull present a picture of considerable morphological interest. In the *Toxochelyinae*, the palate is a primary one; the *Osteopyginae* have a secondary palate; the palate of the *Lophochelyinae* presents a condition intermediate between the two extremes. The palates in these three subfamilies, arranged in a morphological series (fig. 61), illustrate the mode in which the secondary palatal condition arose from the primary one within this family.

The toxochelyid skull (especially that of *Toxochelys latiremis*) has been compared repeatedly (Hay, 1908; Wieland, 1902; Case, 1898) with that of the Recent sea turtles and the snapping turtles. The observers agree that the palatal and pterygoid areas of *Toxochelys* resemble the corresponding regions in *Chelydra*, whereas the basisphenoid, occipital, and quadratal areas compare much more closely with those of the cheloniids. In view of the fact that, obviously, two primary palates (e.g. those of *Toxochelys latiremis* and *Chelydra serpentina*) resemble each other more closely than do a primary and a secondary palate (e.g. those of *Toxochelys* and *Chelonia*), one might be justified in suspecting that the noted similarity between *Toxochelys* and *Chelydra* is merely a superficial one. The skull of *Toxochelys* might be cheloniid in structure throughout, exhibiting, however, a primitive palate.

The fortunate find of a beautifully preserved braincase of *Toxochelys moorevillensis* (C.N.H.M. PR219) furnishes additional evidence in support of the view that the toxochelyid skull combines cheloniid with chelydrid features (pl. 9), as stated by earlier students. The region of the floor of the braincase anterior to the dorsum sellae is chelydrid in its basic construction, whereas the area posterior to the dorsum sellae closely resembles that of *Chelonia* or *Caretta*.

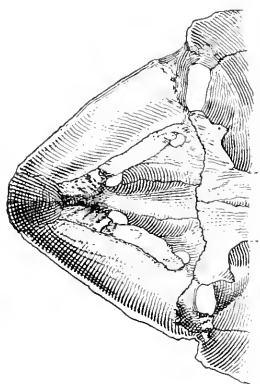
In *Toxochelys*, the basioccipital is visible from the dorsal aspect back to the occipital condyle, a condition found in *Chelonia* only in juvenile forms. In adult individuals, the exoccipitals encroach upon the basioccipital and form a sagittal suture above it (pl. 9). In *Toxochelys* and *Chelonia*, the basioccipital, particularly in its anterior half, forms a sagittal crest (crista basioccipitalis, pl. 9). According to Nick (1912), a cartilaginous knob, the tuberculum basale, rests on this elevation. Anteriorly, the basis tuberculi basalis is formed by a small, acute elevation on the posterior margin of the basisphenoid (pl. 9). The basis tuberculi basalis is tiny in *Chelydra* but very pronounced in *Chelonia* and *Toxochelys*. In the latter, it is more slender and more conspicuous because it is flanked by deep sulci leading to the foramen jugulare anterius (pl. 9). The crista basioccipitalis divides posteriorly into a number of sharp crests that extend, in a postero-lateral direction, to the exoccipitals. In *Chelonia*, similar ridges are but faintly indicated or entirely absent.

Toxochelys latiremis



AMNH 5118

Ctenochelys procox

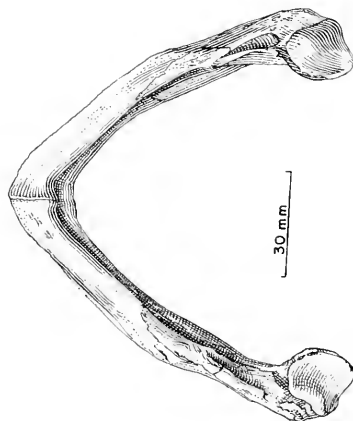


AMNH 6137

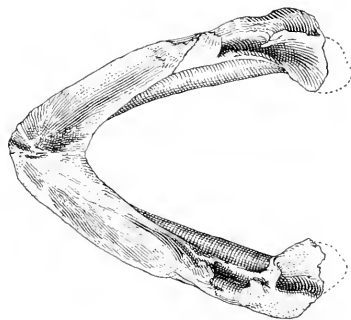
Osteopygis cf. emarginatus



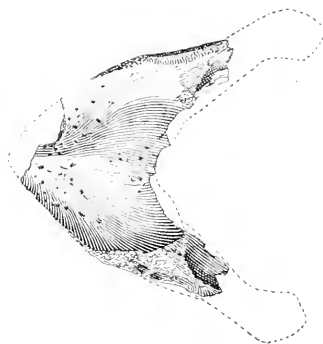
YPM 9136



YPM 3604



AMNH 6137



YPM 913

FIG. 61. Palatal views of skulls and dorsal views of mandibles of *Toxochelys*, *Ctenochelys*, and *Osteopygis*. *Toxochelys* has a secondary palate; *Osteopygis* has a secondary palate; the condition in *Ctenochelys* is intermediate in the sense that there is a beginning of an undershelfing of the choanal passages.

The basisphenoid¹ can, for descriptive purposes, be divided into two portions. The posterior part represents a wide, dorsally concave plate and forms anteriorly the dorsum sellae, with the processus clinoidei on either side of the latter. The anterior portion, the rostrum basisphenoidale, is an ossification replacing the trabeculae baseos cranii and an intertrabecula. In most turtles, the fossa hypophyseos lies at the base of the relatively thin and wide rostrum basisphenoidale, in which case a true dorsum sellae occurs. In cheloniid turtles, the rostrum basisphenoidale is high and narrow and its base is drawn out lengthwise so that there is a notable distance between the fossa hypophyseos and the transverse ridge that is homologous to the dorsum sellae of other forms. In *Toxochelys* the rostrum basisphenoidale resembles that of *Chelydra*, but in *Ctenochelys* the entire basisphenoid compares very closely with that of *Chelonia* (except for a slight difference in the position of the carotid canals; see below). In all cases, including *Chelonia*, a short canal for the passage of the nervus abducens runs on either side, horizontally through the basisphenoid from the base of the rostrum basisphenoidale underneath the processus clinoidei, to the main part of the bone (pl. 9).

The canal for the internal carotid enters on both sides of the skull either by a separate foramen or through an incisura at the ventro-medial corner of the fenestra postotica (fig. 60). In *Chelonia* and *Toxochelys* there is a separate foramen, entirely embedded in the pterygoid. The course of the internal carotid varies considerably among different forms (Siebenrock, 1897; Nick, 1912). In *Chelydra*, *Ctenochelys*, and most probably in *Toxochelys*, the canal runs forward and inward between the pterygoid, the pro-otic and the basisphenoid to the area of the basisphenoid rostrum, but does not join the sulcus cavernosus. There, the internal carotid divides into the arteria cerebrealis, which pierces the rostrum laterally and enters the fossa hypophyseos, and the arteria palatino-nasalis, which follows the lateral margin of the basisphenoid rostrum forward. In *Chelonia*, the internal carotid canal is entirely embedded in the pterygoid posteriorly. Anteriorly, it runs between the pterygoid and the basisphenoid and finally joins the sulcus cavernosus, where the carotid artery divides into the branches mentioned above.

Close to the anterior opening of the abducens canal, there is, in *Chelydra*, a second foramen that, according to Siebenrock (1897), serves for the passage of the nervus vidiani. In *Toxochelys*, this foramen lies farther forward at the bottom of the sulcus cavernosus, and in *Chelonia* it opens into the passageway of the arteria cerebrealis through the lateral wall of the basisphenoid rostrum.

¹ It is now understood that the chelonian basisphenoid is a complex element, representing in many, if not most, turtles a fusion of the basisphenoid proper with a more or less well-developed parasphenoid. In the adult skull, the two components are so intimately united that they appear as one element. In *Chelonia*, only vestiges of a parasphenoid are reported and it is virtually certain that none of the major parts of the fully developed basisphenoid are formed by this dermal element. In *Chelydra*, on the other hand, the floor of the fossa hypophyseos is said to be formed by the parasphenoid. For further detail, see Nick (1912).

The posterior, concave portion of the basisphenoid is divided into lateral halves by a sharp sagittal crest, in *Chelonia*, *Toxochelys*, and *Ctenochelys*. In *Chelydra*, this crest is but faintly indicated (pl. 9, crista basisphenoidalis).

The lower jaws (figs. 60, 61) in the three subfamilies of Toxochelyidae reflect the palatal condition of the skulls. In the Toxochelyinae, the mandible is essentially as in *Chelydra*. The masticatory surface is much narrower at the symphysis than the ventral symphyseal shelf. The masticatory surface is much wider in the Lophochelyinae. At the symphysis, it is as wide as the ventral shelf. In the Osteopyginae, the mandible resembles that of the Recent *Caretta*. The symphysis is very long, probably more than a third of the length of the mandibular ramus (figs. 61 and 85).

Vertebral Column

Wieland (1902) described the cervical vertebrae of *Toxochelys* from a specimen in the Yale collection, Y.P.M. Accession 2491. He came to the conclusion that these vertebrae are "intermediate in character between those of *Chelydra* and the Cheloniidae, being most like the former." In the meantime, another series of cervical vertebrae, complete from the second to the eighth and in rather good state of preservation (pl. 20, fig. A), has become available for study (C.N.H.M. PR123, *Toxochelys latiremis*), as well as a fair number of isolated cervical vertebrae of *Toxochelys moorerillensis*, *Ctenochelys tenuitesta*, and *C. acris*. Furthermore, Williams (1950) has published an extensive paper on the cervical central articulations in living turtles, in which the results of careful observations on a large number of species and individuals are conveniently tabulated. With this excellent ground work at hand, it is now possible to evaluate the characteristics of the cervical vertebrae of *Toxochelys* with accuracy much greater than Wieland could achieve at the time. The available material permits, without doubt, the determination of the pattern of central articulations among Recent turtles to which the Toxochelyidae conform. Using Williams' articulation diagram, the formula for *T. latiremis* (C.N.H.M. PR123) is as follows:

$$(2, (3, (4), 5), 6), 7, 8).$$

In all of the other specimens in which this observation can be made, there is no doubling of the joint surfaces between centra 7 and 8 (eight observations). In none of the specimens is there a plane joint between centra 6 and 7 (seven observations). This would tend to suggest that the most common formula is:

$$(2, (3, (4), 5), 6), 7, 8) \text{ (see Table 1),}$$

with doubling of the joint surfaces between centra 7 and 8 as a variant. The above formula agrees, in detail, with Williams' formula P1, group 2, Dermatemnyidae, Chelydridae (Williams, 1950, p. 552). P2, the second most common pattern for the same group, shows double joints between centra 6 and 7 and between 7 and 8. Doubling of only the posterior one of these joints (as in C.N.H.M. PR123) is apparently not known in Recent chelydrids.

TABLE 1.—PATTERN OF CENTRAL ARTICULATION IN
CERVICAL VERTEBRAE OF TOXOCHELYIDAE

Species	Numbers of Vertebrae						
	2	3	4	5	6	7	8
<i>Toxochelys latiremis</i>							
PR123.....	(2(,	(3(,	(4),)5),)6),)7),)8)*
<i>Toxochelys moorevillensis</i>							
P27391.....)7),)8)*†
PR28.....)7),)8)*
P27550.....)8)
<i>Lophochelys natatrix</i>							
PR220.....)8)*
<i>Ctenochelys tenuitesta</i>							
P27351.....)8)*
P27548.....)8)*
P27361.....)6)		
PR248.....)6)		
<i>Ctenochelys acris</i>							
PR97.....)5),)6))8)†
PR137.....)8)†
P27354.....)6)		

* Centrum of 8 short. † Centrum of 8 long.

‡ Slight indication of doubling between 7 and 8; ribs on 8.

TABLE 2.—MEASUREMENTS AND INDICES OF CERVICAL VERTEBRAE IN
CHELYDRA, TOXOCHELYS AND CHELONIA

(Indices in *italics*)

Species	Cervical vertebrae						
	2	3	4	5	6	7	8
	Length of centra						
<i>Chelydra serpentina</i> *	24.5	30.0	39.5	33.0	32.0	32.0	22.0
	100.	122.	161.	135.	131.	131.	90.
<i>Toxochelys latiremis</i> †	21.5	23.0	31.0	22.5	27.0	27.5	19.0
	100.	107.	144.	105.	126.	128.	88.
<i>Chelonia mydas</i> ‡	40.0	46.0	68.0	46.5	46.0	62.0	30.0
	100.	115.	170.	116.	115.	155.	75.
Species	Length of neurapophyses						
	2	3	4	5	6	7	8
	Length of centra						
<i>Chelydra serpentina</i> *	26.5	19.0	21.5	21.0	15.0	14.5	18.5
	108.	78.	88.	86.	61.	59.	76.
<i>Toxochelys latiremis</i> †	22.5	14.0	16.5	16.0	18.5	22.5	22.5
	105.	65.	77.	74.	86.	105.	105.
<i>Chelonia mydas</i> ‡	49.5	29.5	25.0	19.0	21.0	33.0	37.0
	124.	74.	63.	48.	53.	83.	93.
Species	Width of postzygapophyses						
	2	3	4	5	6	7	8
	Length of centra						
<i>Chelydra serpentina</i> *	20.0	21.0	21.0	22.0	19.0	22.5	27.0
	82.	86.	86.	90.	78.	92.	110.
<i>Toxochelys latiremis</i> †	26.5	26.0	30.0	30.5	26.5	21.0	23.0
	123.	121.	140.	142.	123.	98.	107.
<i>Chelonia mydas</i> ‡	35.0	42.0	49.5	51.0	37.0	42.0	48.0
	88.	105.	124.	128.	93.	105.	120.

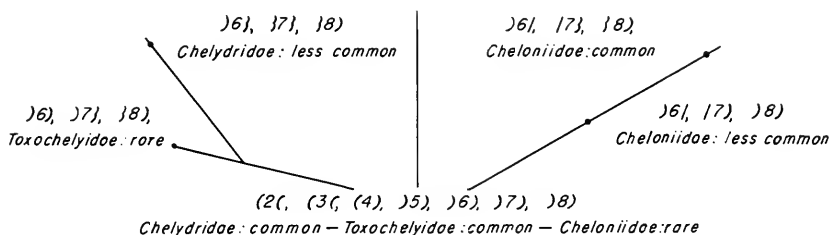
* Specimen in private collection (No. 21). † C.N.H.M. PR123.

‡ C.N.H.M. 22066. || Approximate.

All indices calculated as follows: value $\times 100/\text{length of centrum of second vertebra}$.

Rarely, a formula identical with P1 occurs in Recent cheloniid turtles (Williams, N3, group 3, Cheloniidae, Dermochelyidae). Normally, however, there is a plane joint between centra 6 and 7, and the two vertebrae may even fuse entirely (e.g. in *Chelonia mydas*, C.N.H.M. 22066). The joint surfaces between centra 7 and 8 are usually double in cheloniids.

There can be little doubt that double articulation surfaces and plane joints are specializations tending to reduce the movability of the neck at specific points. The fact that plane joints may even disappear by fusion of the adjoining centra would certainly indicate that they are not to be considered as morphologically intermediate conditions between amphicoelous and pro- or opisthocelous joint surfaces. In view of the vast amount of evidence gathered by Williams (1950), it would seem reasonable to assume that, depending on whether the intercentral cartilage mass becomes attached to the preceding or the succeeding of two amphicoelous centra, pro- or opisthocelous vertebrae develop directly, not via an intermediate plane-jointed condition. If we thus interpret double articulations and plane joints as specializations, the following formulae and their relative frequency of occurrence present an interesting picture:



The P1 formula, here interpreted as primitive in the three families, occurs in all three groups. In the Cheloniidae, it is rare and the greatest number of individual variants fall within the specialized patterns. In the Chelydridae and Toxochelyidae, P1 is the most common individual variant; the much less frequent, specialized variants differ, however, possibly indicating trends in different directions, since the less specialized toxochelyid variant does not seem to occur in the chelydrids. Even though the number of observations on toxochelyid turtles is still limited, the facts are at least suggestive.

If the relative lengths of the cervical centra, the neurapophyses, and the widths of the latter across the posterior zygapophyses are compared with the corresponding dimensions in *Chelydra* and *Chelonia* (fig. 62) it would seem that *Toxochelys* exhibits a type of cervical differentiation peculiar to itself (see Table 2). A noteworthy feature is the difference in the relative length of the centrum of the eighth cervical vertebra in various species of the Toxochelyidae (see Table 3).

Of the thoracic vertebrae, individual centra and detached neurapophyses are associated with a number of specimens, and neurapophyses occasionally remain attached to neural plates. The centra are wider than high and, as usual,

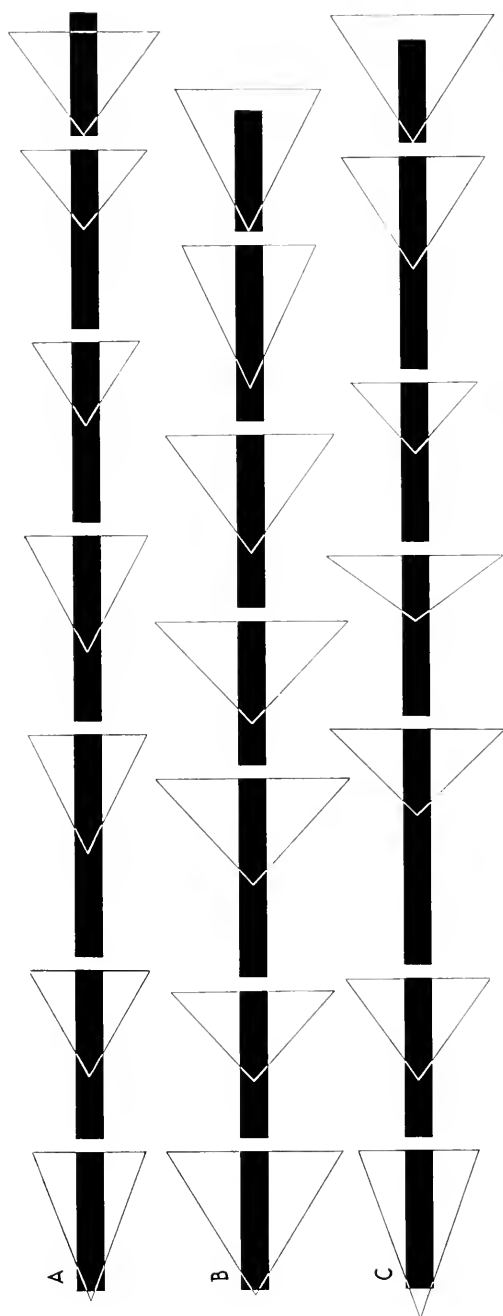


FIG. 62. Diagram showing relative size relationships in cervical vertebrae of A, *Chelydra serpentina*, B, *Torochelys latiremis*, and C, *Chelonia mydas*. Black bars = lengths of cervical centra 2 to 8; triangles = lengths and widths of neural arches at postzygapophyses.

are notably narrower at mid-length than at the ends. The centra are hollowed out lengthwise to form the ventral half of the neural canal, as in *Chelydra*. The ninth, or first shell vertebra, is represented by a number of specimens. The centrum is short and broad, ventrally keeled. On either side, there is a small notch separating the articulation facet of the reduced first rib from that of the large second rib (fig. 63). In *Chelydra*, these facets are very close together, and in some specimens the ribs are proximally and distally in contact. In Recent cheloniid turtles, the two described facets are spaced much farther apart (fig. 63).

The neurapophyses of the typical shell vertebrae are thin and probably similar to those in *Chelydra*, though they are invariably distorted and difficult to compare. A few well-preserved vertebrae from the area directly preceding the sacral vertebrae are available in *Toxochelys moorevillensis* C.N.H.M. P27391. There is a close degree of similarity between the centra of these elements and those of *Chelydra*, but a sharp difference in the size of the neurapophyses. The latter are relatively stout and strong. They are free from the carapace and the most anterior of the five available elements forms strong diapophyses for the attachment of the ribs. Closer to the sacral region, the transverse processes, as in *Chelydra*, are synapophyses, formed jointly by the neural arches and the centra. Some of the surfaces with which these centra articulate are strongly concave and convex, rather than plane. This, coupled with the fact that the neurapophyses are free from the carapace, would indicate that there was a certain amount of movability of the vertebral column in front of the pelvis, which is an unusual situation.

The sacral region of *Toxochelys* consists of three vertebrae instead of two, as in *Chelydra*. These are free from the carapace and bear strong, distally expanded ribs. The size of these ribs increases notably from the first to the third.

TABLE 3.—MEASUREMENTS AND INDICES OF EIGHTH CERVICAL CENTRUM IN TOXOCHELYIDAE

Species	Eighth cervical centrum		
	Length* mm.	Width† mm.	Index
<i>Toxochelys latiremis</i>			
PR123.....	18.5	12.0	64.8‡
<i>Toxochelys moorevillensis</i>			
P27550.....	19.0	11.0	57.9
P27391.....	15.5	12.5	80.6
PR28.....	11.0	10.0	90.9
<i>Lophochelys natatrix</i>			
PR220.....	6.0	5.0	82.2
<i>Ctenochelys tenuitesta</i>			
P27351.....	18.0	13.0	72.2
P27548.....	21.5	15.0	69.7
<i>Ctenochelys acris</i>			
PR137.....	27.0	14.0	51.8
PR97.....	36.0	±19.0	52.8

* Length: distance from depth of anterior facet to peak of posterior facet.

† Width: measured at narrowest point of centrum.

‡ Low index due to double anterior joint surface in this individual.

In contrast to the presacral vertebrae, the centra of the sacral elements are ventrally keeled, exactly as in *Chelydra*. The centrum of the (?)second sacral vertebra of *T. moorevillensis* (C.N.H.M. P27391) is plane in front and strongly convex behind. The transverse processes are synapophyses with the larger portion of the joint surfaces formed by the neural arches.

The caudal region of the vertebral column is not yet adequately known and the available evidence is somewhat confusing. In general shape, the tail vertebrae correspond with those of *Chelydra* except that they all are procoelous throughout and comparison reveals a number of details in which these vertebrae resemble those of *Chelonia*. An entire caudal series is not known in any toxochelyid, but in one specimen of *T. moorevillensis* (C.N.H.M. P27391), there are three vertebrae; in another (C.N.H.M. PR136), there are two; in *Ctenochelys tenuitesta* (C.N.H.M. P27351), there are two; and in *C. acris* (C.N.H.M. P27352), there are five. All of these vertebrae, except those of C.N.H.M. P27391, can be compared rather closely with the posterior caudals of *Chelydra* (save for being procoelous) or *Chelonia*. They suggest a rather long tail much as in *Chelydra* and probably longer than in *Chelonia*. The vertebrae of C.N.H.M. P27391, however, do not seem to agree with this picture. The three vertebrae are small, yet, compared to the tail series of *Chelydra*, they appear to belong to the anterior third rather than to the posterior region of the tail. These vertebrae had distinct ribs attached chiefly to their neurapophyses and the size of the centra is not greatly different from that of the sacral vertebra in this specimen (see above). All this would tend to indicate that the three vertebrae here discussed are anterior tail elements. But they seem much too small to have been followed by vertebrae the size of those of C.N.H.M. PR136, an individual whose shell is scarcely larger than that of C.N.H.M. P27391. In *Chelydra*, there is a slight increase in the length of the centra from the first caudal to about the sixth (in C.N.H.M. 22056, from 13.5 mm. to 19.0 mm.); thereafter the centra gradually decrease in length. If a similar situation should prevail in *Toxochelys*, we should have to assume an increase of centrum length from about 12 mm. to 21 mm., judging from the materials of C.N.H.M. P27391 and PR136. While these figures do not seem inconceivable, they do not present the over-all size relationship between the vertebrae, and direct comparison of the elements certainly gives the impression that they could not possibly have occurred in the same caudal series. The most plausible explanation is the assumption that a marked sexual dimorphism in the tail length of *Toxochelys* existed, a condition not without parallel in Recent turtles (e.g. in the Trionychidae).

Carapace and Plastron

As usual, the shell is the most frequently preserved part of the skeleton and is consequently the best known part. The state of preservation varies greatly even among individuals buried in the same formation and locality. Comparison between well and poorly preserved shell remains is often possible only if large collections are at hand.

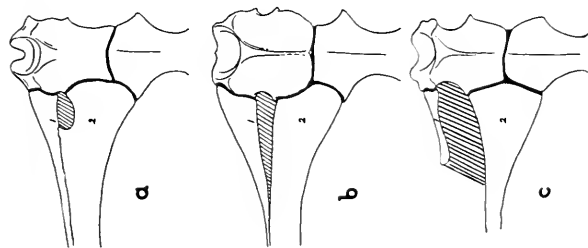


FIG. 63. Comparison of centra of first and second shell vertebrae with their ribs in (a) *Chelydra serpentina*, (b) *Tenochelys tenitesta* (p27361), and (c) *Erethmochelys imbricata*.

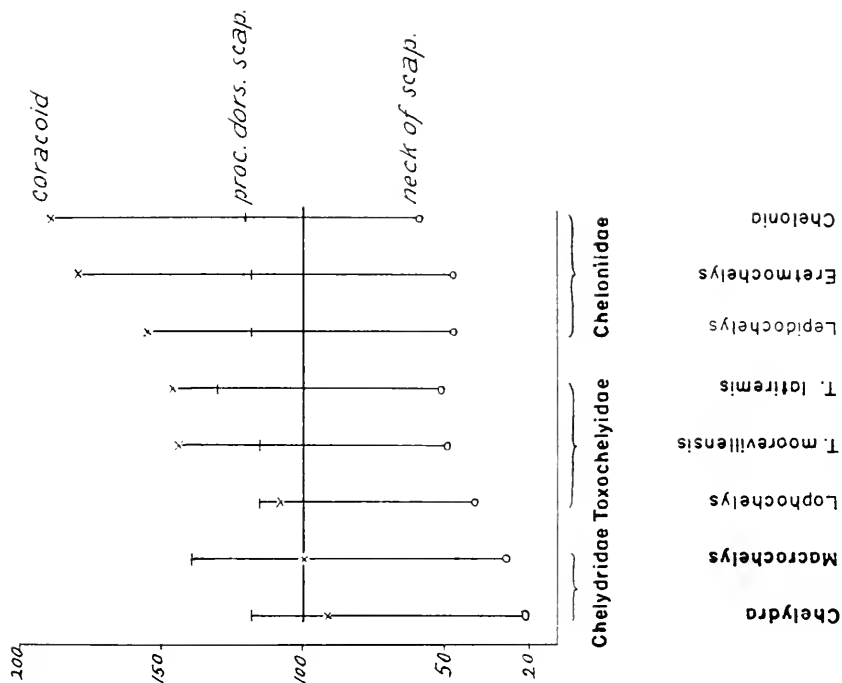


FIG. 64. Proportional differences in shoulder girdles of chelydrid, toxochelyid, and chelonid turtles.

The morphology of the toxochelyid shell shows, as does the rest of the skeleton, similarities both to the chelydrids and cheloniids, and there is no single feature that would distinguish it at once from these groups.

The carapace of the Toxochelyidae is circular, oval, or broadly cordiform. It is either smooth (not broadly tuberculated as in the Chelydridae), or it is provided with a sharp mid-dorsal carina, formed by the normal number of neural plates (8-10), usually in conjunction with epithecal ossicles. The neural series is always normal; there is no tendency toward reduction of these plates as in the Thalassemyidae, or toward fragmentation into many supernumerary elements as in cheloniid turtles. Successive neurals are hexagonal, rather narrow and of similar outline, never expanded transversely or differentiated into alternating octagonal and rectangular plates as in the Recent Chelydridae. A pre-neural element occurs in some species. The nuchal plate lacks lateral processes such as those in the Chelydridae, and the ventral boss of the cheloniid, dermo-chelyid and protostegid nuchal is small, insignificant or entirely wanting. The peripheral plates are nearly always well developed; they may or may not be suturally attached to the costal plates. The rib of the first costal plate always forms a pit in the third peripheral, never in the fourth, as in some cheloniid turtles. The peripheral edge of the shell may be even or serrated, but these two conditions are always correlated with the differentiation of the neural series; flat, uncarinated forms have an even, unserrated carapacial edge, whereas all carinated genera have a serrated peripheral edge. Typically, there are two large suprapyrgals; the lower one, however, may be greatly reduced.

The plastron is cruciform, essentially chelydrid in shape and construction, but the axillary and inguinal notches are not as large as in *Chelydra*. The width of the plastral bridge (hyo- and hypoplastron) at the narrowest point amounts to about 17 per cent of half the width of the plastron in *Chelydra*. The comparable value ranges, in the Toxochelyidae, from 35 per cent, in forms with circular to oval shells, to 60 per cent in elongated species. In the Cheloniidae, it ranges from 55 per cent in forms with more or less circular outline to 110 per cent in species with greatly elongated, cordiform carapaces (see Table 4). In all known toxochelyid species, the epiplastra are small, relatively insignificant elements in contrast to those in the Cheloniidae, which are as well developed as the xiphiplastra. Hyo-, hypo-, and xiphiplastra form, parasagittally, two more or less distinct keel ridges to which keel bosses are added in the more specialized genera.

Girdles and Limbs

The toxochelyid shoulder girdle is cheloniid in shape, resembling most closely that of the Recent *Lepidochelys*. The scapula has a definite neck area between the glenoidal and coracoidal facets and the base of the bifurcation. In chelydrid turtles, this neck area is wanting. The coracoid is distally expanded as in *Lepidochelys* and generally resembles this form quite closely. The length relationships between the neck, the medial and dorsal processes of the scapula

TABLE 4.—COMPARISON OF THE RANGE OF INDICES IN THE PLASTRON OF
THALASSEMYIDAE, CHELONIIDAE AND TOXOCHELYIDAE

Index = axillo-inguinal distance \times 100 half width of plastron

Thalassemyidae	
<i>Idiochelys fitzingeri</i> (Lortet, 1892)	93
<i>Thalassemys marina</i> (from Fraas, after Abel, 1919)	93
Cheloniidae	
<i>Lepidochelys kempfi</i> , C.N.H.M. 31334	55
<i>Chelonia mydas</i> , C.N.H.M. 22066	97.5
<i>Eretmochelys imbricata</i> , C.N.H.M. 22242	100
<i>Catapleura arkansaw</i> , C.N.H.M. P27045	72
" <i>Lytoloma</i> " <i>longiceps</i> (Owen 1849-84, vol. 2, pl. 13)	82
<i>Argillochelys subcristata</i> (Owen 1849-84, vol. 2, pl. 10)	86
<i>Argillochelys convexa</i> (Owen 1849-84, vol. 2, pl. 14)	98
" <i>Lytoloma</i> " <i>planimentum</i> (Owen 1849-84, vol. 2, pl. 16)	98
<i>Protosphargis veronensis</i> (from Capellini, after Abel, 1919)	107
Toxochelyidae	
<i>Toxochelys barberi</i> , C.N.H.M. P27047	37
<i>Toxochelys moorevillensis</i> , C.N.H.M. P27330	39
C.N.H.M. P27348	45
<i>Toxochelys latiremis</i> , K.U.(V.P.) 1244	40
<i>Toxochelys weeksi</i> , U.T. K20	43
<i>Thinochelys lapisossea</i> , C.N.H.M. P27453	42
<i>Osteopygis emarginatus</i> , Y.P.M. 783	47
<i>Porthochelys laticeps</i> , K.U.(V.P.) 1204	53
<i>Lophochelys natatrix</i> , C.N.H.M. PR220	57
<i>Ctenochelys stenopora</i> (type material)	57
U.S.N.M. 6013	58
A.M.N.H. 6137	47
<i>Ctenochelys tenuitesta</i> , C.N.H.M. P27551	59

and the coracoid are illustrated in figure 64. The dorsal process of the scapula is much longer than the coracoid in the chelydrid turtles. In the Toxochelyidae (except in juvenile forms), it is shorter. In the Cheloniidae, the coracoid is enormously elongated (see Table 5).

In contrast to the shoulder girdle, the pelvis is chelydrid in shape (fig. 65). The most obvious difference between the chelydrid and cheloniid pelvis lies in the relative sizes of the pubes and ischia. In the cheloniid turtles, the ischia are diminutive compared to the pubes and the strong posterior processes of the chelydrid ischia are either absent (e.g. in *Chelonia mydas*, C.N.H.M. 22066) or exceedingly small (fig. 65). The toxochelyid ischium is quite large (figs. 65 and 66 and Table 6) and the posterior process is even more pronounced than in *Chelydra*. In *Toxochelys moorevillensis*, the shape of the pubis is highly variable with regard to the size and shape of the anterior notch and the width of the antero-lateral process (fig. 65), which is wider than in *Chelydra* but not much wider than in *Macrochelys*. The pubes of C.N.H.M. PR166 (fig. 65) show, furthermore, that the antero-lateral process pointed ventrad as in Chelydridae; in cheloniid turtles, it lies in the same plane as the symphyseal portion of the

pubis. The anterior notch is deeper than in the Cheloniidae. The ilia of *Toxochelys* also compare rather more closely with those of *Macrochelys* than with any cheloniid. The dorsal portion, attached to the sacral ribs, is long and very rugose medially. In cheloniid species, this dorsal process of the ilium is short and not notably rugose medially. Instead, there is a dorso-lateral rugosity that contacts the carapace. Nothing comparable is seen in *Toxochelys*.

Limbs that are articulated or even partially articulated are unknown in toxochelyid turtles. A forelimb of *Toxochelys latiremis* was described and figured by Wieland (1902), but it was not articulated and there are some doubts as to the correctness of the reconstruction. Isolated limb-bones are associated with many specimens, but only rarely is there enough material to permit identification and to justify detailed description and comparison.

TABLE 5.—MEASUREMENTS AND INDICES OF SHOULDER GIRDLE IN
CHELYDRIDAE, TOXOCHELYIDAE AND CHELONIIDAE

Species	Value a	Index	Value b	Index	Value c	Index	Value d	Index
Chelydridae								
<i>Chelydra serpentina</i> *	80.5	100	17.0	21.1	95.0	118.0	73.0	90.7
<i>Macrochelys temminckii</i> C.N.H.M. 22060.....	108.0	100	30.0	27.7	150.0	138.8	108.0	100.0
Toxochelyidae								
<i>Toxochelys latiremis</i> Y.P.M. 3602.....	26.0	100	13.5	51.9	34.5	132.7
C.N.H.M. PR123.....	94.0	100	48.0	51.0	122.0	129.7	137.0	145.7
<i>Toxochelys moorevillensis</i> C.N.H.M. PR136.....	±87.0	100	42.5	48.8	100.0	114.9 ± 125.0	143.6
<i>Lophochelys natatrix</i> C.N.H.M. PR220 (juv.)	34.3	100	13.5	39.4	39.4	114.8	37.0	107.8
<i>Ctenochelys stenopora</i> A.M.N.H. 6137.....	74.0	100	34.5	46.6	88.0	118.9
Cheloniidae								
<i>Lepidochelys kempi</i> C.N.H.M. 31334.....	76.0	100	35.5	46.7	90.0	118.4	118.0	155.2
<i>Eretmochelys imbricata</i> C.N.H.M. 31009.....	66.0	100	31.0	46.9	78.0	118.1	119.0	180.3
<i>Chelonia mydas</i> C.N.H.M. 22066.....	153.0	100	89.0	58.1	183.0	119.6	304.0	198.7

Value a=length of ventral prong of scapular fork, measured from tip of process to edge across neck of scapula.

Value b=length of scapular neck, measured from base of fork to ridge dividing glenoidal facet from coracoidal suture face.

Value c=length of dorsal prong of scapular fork, measured from tip of process to edge across neck of scapula.

Value d=maximal length of coracoid.

All indices are calculated as follows: value $\times 100/\text{value } a$

* Private collection (No. 21).

On the basis of a comparative study of the turtle humerus (1900) and the forelimb (1902) of *Toxochelys*, Wieland concluded that the limbs of the Toxochelyidae were primitive sea-turtle flippers, but that they indicated, with more or less distinctness, a *Chelydra*-like ancestry. Comparison of various features

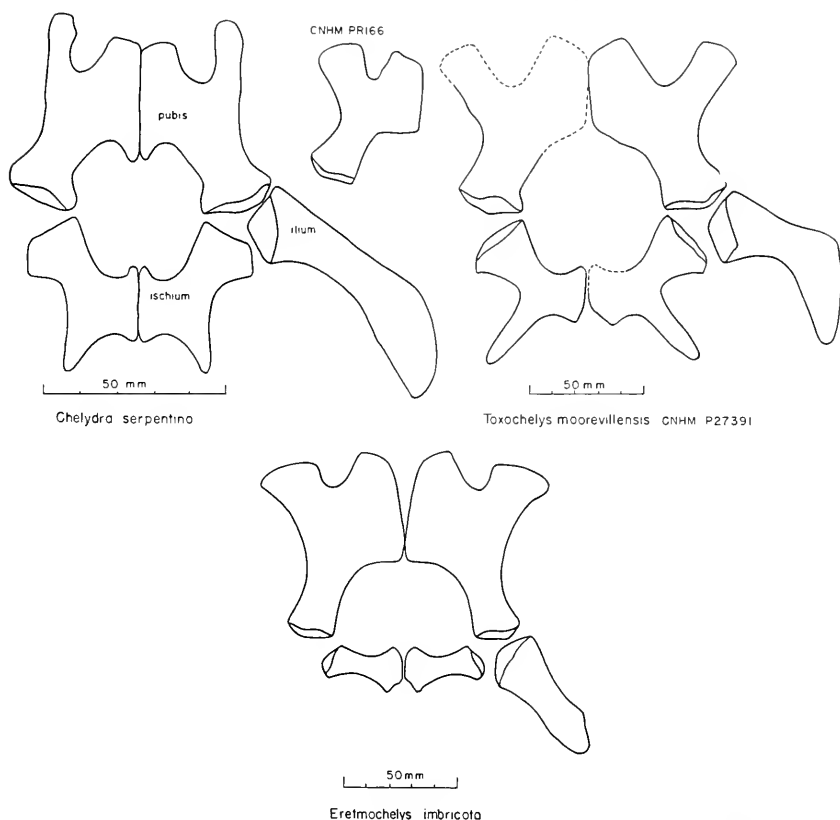


FIG. 65. Comparison of pelvises of *Chelydra*, *Toxochelys*, and *Eretmochelys*. C.N.H.M. PR166, pubis of another specimen of *T. moorevillensis*.

of the forelimb reveals a definite mixture of resemblances to the sea turtles on the one side and the chelydrids and trionychids on the other. To this extent, Wieland's analysis was correct. There is, however, a profound difference in the type of locomotion between sea turtles and fresh-water turtles. If the *Toxochelyidae* present an intermediate condition, as the morphology seems to suggest, a more detailed analysis of the problem is required.

MORPHOLOGY AND FUNCTION OF THE LIMBS IN FRESH-WATER TURTLES: All fresh-water turtles propel their bodies by means of lateral strokes of the limbs. In some cases, all four limbs are actively used (*Chelydridae*, *Kinosternidae*, *Trionychidae*); in others, the hind limbs alone act as paddles and the forelimbs are held tightly against the body during swift locomotion (*Emyidae*, particularly *Graptemys*, *Pseudemys*, etc.). In all instances, the right and left

TABLE 6.—MEASUREMENTS* AND INDICES OF SURFACE AREAS OF ISCHIUM AND PUBIS IN CHELYDRA, ERETMOCHELYS AND TOXOCHELYS

	Pubis, mm. ²	Index	Ischium, mm. ²	Index
<i>Chelydra serpentina</i>				
Private specimen (No. 21).....	2174	100	1322	60.8
<i>Eretmochelys imbricata</i>				
C.N.H.M. 22352.....	2217	100	331	14.9
<i>Toxochelys moorevillensis</i>				
C.N.H.M. P27391.....	2308	100	1069	46.3

*The mm.² count was made on outline drawings of the bones, obtained by photographic means and enlarged to about the same over-all size. Outline drawings illustrated in figure 66.

hind limbs and/or forelimbs are used in alternate fashion, never (to my knowledge) simultaneously. The paddle surfaces of the hind limbs are larger than those of the forelimbs, and the greater size tends to indicate that they are the more important organs of propulsion. Both fore- and hind limbs are retractable, that is, they can be folded up. In the retracted forelimb, the humerus points forward and inward; the remainder of the limb turns backward sharply at the elbow joint and lies nearly parallel to the humerus. The hind limb can be folded up at two points, the knee and the ankle. In the retracted position, the femur and the pes point forward and outward, the zeugopodium backward and inward.

The type of locomotion and the range of movability of the limbs of fresh-water turtles are reflected in the structure of the limb bones. The hind limbs are usually somewhat longer than the forelimbs (fig. 67). The humerus is an "S"-curved bone, with the head standing nearly at a right angle to the main axis of the shaft (fig. 68). The curvature in the distal two-thirds of the bone is not as pronounced as near the proximal end and varies notably in different genera. The distal joint surface extends in a marked elevation onto the ventral¹ face, thus permitting extreme bending of the limb at the elbow joint. The principal movement of the humerus is in a horizontal plane that forms a very small angle (about 10° in *Chelydra*, fig. 69) with the main axis of the humeral shaft. As Wieland (1900) has pointed out, the radial process lies at the level of the caput humeri. Radius and ulna are located, side by side, in the plane of the manus and form a typical spatium interosseum. The radius is slightly shorter than the ulna. The carpus consists of numerous, nearly spherical bones that permit a great deal of movement in this region. The manus differs somewhat among genera. As a rule, digits 1, 2, and 3 are the most robust and bear strong claws. The remaining digits may bear claws or lack them as in trionyhid turtles, where even a moderate polyphalangy may occur on digits 4 and 5 (for example, in *Trionyx cartilagineus*, C.N.H.M. 11088, the phalangeal formula is 2, 3, 3, 4, 4). Digits 3 (*Chelydra*) or 4 (*Trionyx*) may be the longest.

The femur of fresh-water turtles is usually longer than the humerus (see Table 7). Tibial and fibular trochanters are separated by a deep "V"-shaped depression. The proximal ends of these processes have cartilage-covered surfaces

¹ The morphologically ventral side of the humerus of fresh-water turtles faces postero-laterad in the animal.

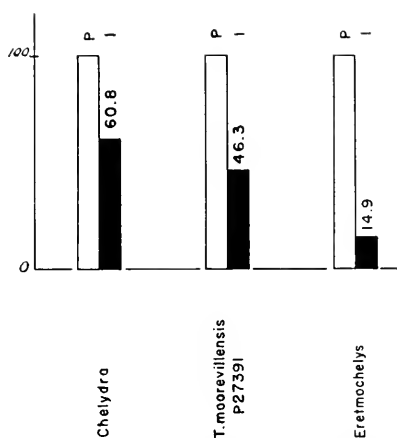


FIG. 66. Indices of pubic-ischial surface areas in *Chelydra*, *Toxochelys moorevillensis*, and *Eretmochelys*.

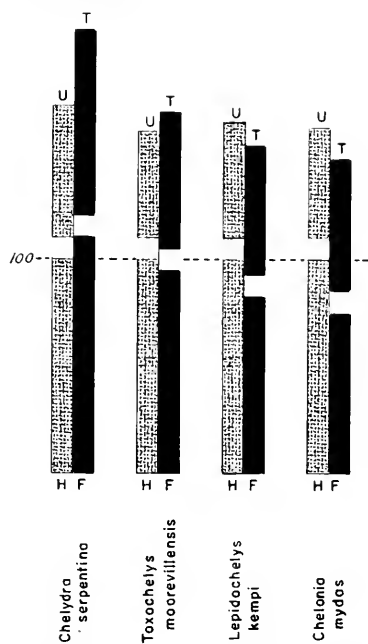


FIG. 67. Limb proportions in *Chelydra*, *Toxochelys*, and cheloniid turtles. Shaded columns=forelimbs (H, humerus; U, ulna); black columns=hind limbs (F, femur; T, tibia).

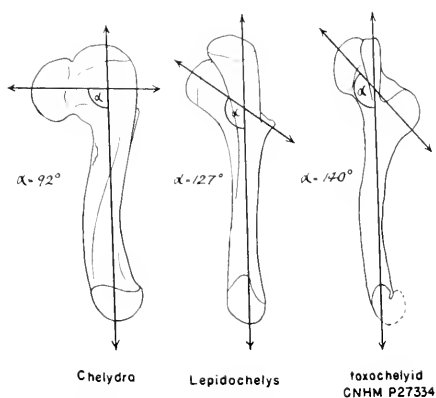


FIG. 68. Comparison of angle α in humeri of *Chelydra*, *Lepidochelys*, and a toxochelyid.

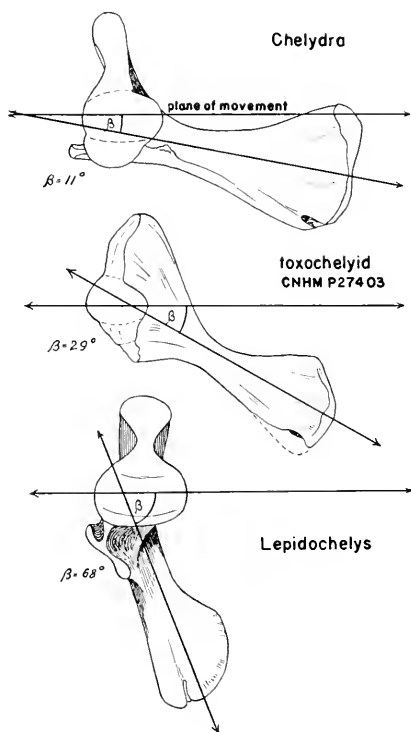


FIG. 69. Comparison of angle β in humeri of *Chelydra*, *Lepidochelys*, and a toxochelyid.

that are connected with the head of the femur (fig. 70). Tibia and fibula are very long (fig. 67). In *Chelydra*, the fibula has distally a thin, laterally projecting ridge. The tarsus is provided with intertarsal joint surfaces extending to the dorsal faces of the tarsal elements, thus providing the required range of movement for the retraction of the pes. The latter, in retracted position, is bent forward against the zeugopodium. The foot of fresh-water turtles is specialized on the fibular side. Phalanges 1, 2, and 3 are large and bear claws. Metatarsal V is enlarged and stands at an angle of about 55° to the main axis of the pes and is movable against distal tarsal 3+4. Metatarsal IV rests against metatarsal V. The mechanism permits the fourth and fifth toes to be spread away from the third and to tighten the large webs between these toes. The fifth digit has four phalanges in *Chelydra*.

The limbs of the fresh-water turtles are, of course, not exclusively swimming organs. They also serve for walking on land and for digging, and the forelimbs are often used to aid in feeding. The fresh-water type of aquatic locomotion is highly developed in the Trionychidae and amazingly efficient as regards speed.

MORPHOLOGY AND FUNCTION OF THE LIMBS IN SEA TURTLES: The type of locomotion in sea turtles differs greatly from that of fresh-water turtles. In all

TABLE 7.— HUMERUS-FEMUR PROPORTIONS IN FRESH-WATER TURTLES, SEA TURTLES AND TOXOCHELYID TURTLES*

Fresh-water turtles	Femur
<i>Glyptops plicatulus</i> , A.M.N.H. 336	114.3
<i>Baena riparia</i> , A.M.N.H. 5977	101.1
<i>Chelydra serpentina</i> , private specimen (No. 21)	109.1
<i>Chelydra serpentina</i> , C.N.H.M. 22058	103.2
<i>Sternotherus odoratus</i> , C.N.H.M. 31278	105.8
<i>Trionyx ferox</i> , C.N.H.M. 31014	103.0
<i>Trionyx muticus</i> , C.N.H.M. 22065	109.4
<i>Pseudemys floridana</i> , C.N.H.M. 22473	112.1
Sea turtles	
<i>Lepidochelys kempi</i> , C.N.H.M. 31334	92.1
<i>Eretmochelys imbricata</i> , C.N.H.M. 31009	71.8
<i>Protostega gigas</i> (from Wieland, 1906)	79.8
<i>Dermochelys coriacea</i> (from Wieland, 1906)	72.8
Toxochelyid turtles	
<i>Toxochelys latiremis</i> , Y.P.M. 3602	91.9
<i>Osteopygis emarginatus</i> , Y.P.M. 783	105.2

* Humerus = 100.

cheloniid, dermochelyid and protostegid turtles, the forelimbs are the principal organs of locomotion; the hind limbs are used only for steering during straight propulsion. The forelimbs, specialized flippers, are longer than the hind limbs and propel the body by *simultaneous, vertical* strokes. A sea turtle "flies" through the water. Neither the flippers nor the hind limbs are retractable; that is, they cannot be folded up as in fresh-water turtles. In contrast to the forelimbs of fresh-water turtles, the sea-turtle flippers are almost exclusively organs of propulsion. The propulsion speed is slow compared to that of trionychid turtles,

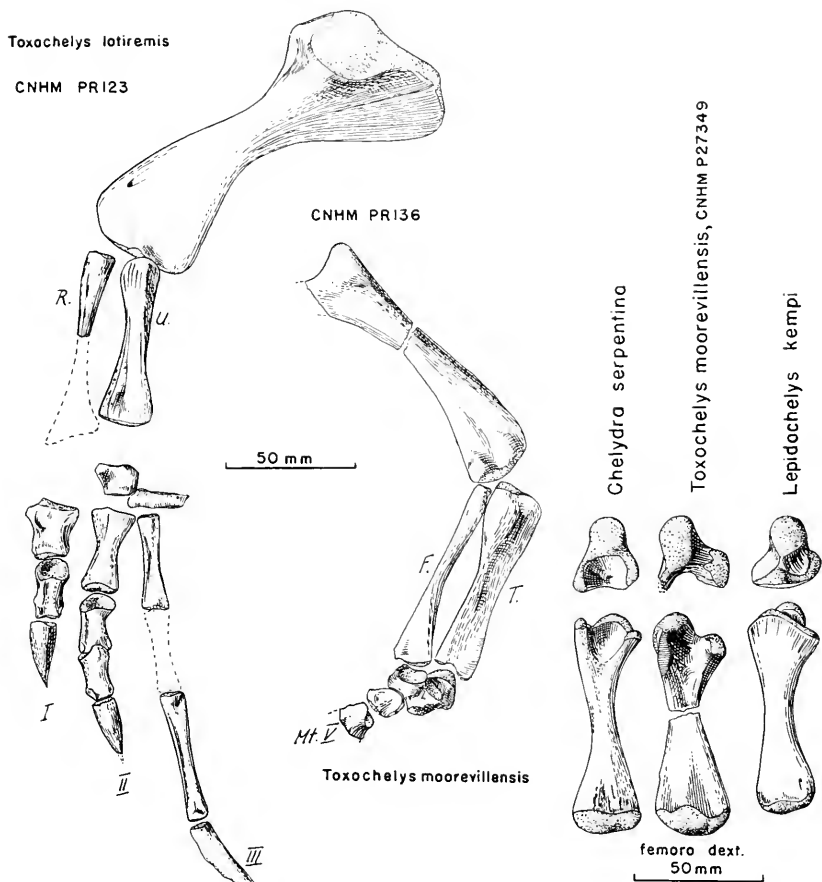


FIG. 70. Forelimb of *Toxochelys latiremis* (C.N.H.M. PR123; elements of third digit may not be correctly placed); hind limb of *Toxochelys moorevillensis* (C.N.H.M. PR136); comparison of right femora of *Chelydra*, *Toxochelys*, and *Lepidochelys*.

but the limbs of the latter are put to intermittent use, whereas those of the sea turtle are in continuous, slow motion during most of the waking hours of the individual.

The peculiarities of the sea-turtle type of locomotion are clearly reflected in the limb skeleton. The flipper is conspicuously longer than the hind limb. The humerus, longer than the femur (see Table 7), moves in a vertical plane and is almost straight. The angle between the axis of the caput humeri and the shaft is about 127° in *Lepidochelys kempfi* (fig. 68). The surface of the distal joint is restricted, thus permitting only a moderate amount of movement at the elbow.

The angle between the axis of the shaft and the principal plane of movement of the humerus in *Lepidochelys* is 68° (fig. 69), as against 11° in *Chelydra*. As Wieland (1900) stated, the radial process is located on the shaft more distally than in fresh-water turtles.

In the zeugopodium, the radius is much the longer of the two bones (see Table 8). Radius and ulna do not lie side by side in the plane of the manus; instead, the ulna lies above the radius in a plane more or less rectangular to that of the manus. Near its distal end, the ulna is attached to the radius by means of a contact rugosity. The carpus is characteristically modified. Intermedium and ulnare of the proximal carpal row are greatly elongated and dorso-ventrally flattened, as are all of the carpal elements except the radiale and the distal carpal I. The joint surfaces of all of the carpal elements are flat and sharply restricted in the proximo-distal and transversal contact areas of adjoining elements. In old individuals of *Chelonia*, the distal carpals on the ulnar side fuse to form a solid, thin, transverse plate. Very little movement is thus possible in this area.

Metacarpals and phalanges are much elongated. All of the fingers, including the first, which bears a strong, curved claw, are firmly included in the flipper and therefore not capable of separate movement. The manus is stiffened by tight dorsal and ventral ligaments and by tough skin that forms large, horny scales along the edges. The third is the longest digit in the flipper.

The hind limb, specialized as a steering organ, is characterized by the relatively great width of the tarsus and the pes and by a peculiarity at the proximal end of the femur. In fresh-water turtles, the femoral trochanters are separated by a depression. In sea turtles, there is no trace of a depression and the cartilage-covered proximal surfaces of the trochanters form a continuous ridge opposite the head of the femur (fig. 70). Tibia and fibula are straighter than in fresh-water turtles, thus leaving a much narrower spatium interosseum between them. The fibula is thick distally, lacking a thin lateral ridge as in *Chelydra*. In old individuals of *Chelonia*, the tarsal bones undergo extensive fusion, so that only three compound elements remain. In a near-adult specimen of *Lepidochelys*, there are six tarsal elements; namely, a tibiale + intermedium + centrale, a fibulare, and four distal tarsals. The fourth is greatly enlarged and represents, probably, a fusion of distal carpals 4 + 5. In the specimen of *Chelonia* mentioned above, the two proximal elements of the *Lepidochelys* tarsus have fused into one large ossicle. Distal tarsals 1 and 2 are fused and distal tarsal 3 is fused to the enlarged fourth element. Metatarsi I and V are much enlarged, giving the pes its great width. Digits 2, 3, and 4 are moderately elongated, the third being the longest. The end phalanx of the first digit bears a large claw. Nearly all elements of the tarsus and the pes are dorso-ventrally flattened.

THE MORPHOLOGY OF THE LIMBS AND THE PROBABLE TYPE OF LOCOMOTION IN THE TOXOCHELYIDAE: The morphology of the limbs of *Toxochelys*, compared to that of the Chelydridae and Cheloniidae, presents a very interesting picture.

Briefly, it may be stated that the forelimb is a primitive sea-turtle flipper, whereas the hind limb is chelydrid throughout its known parts.

Even though the over-all length of the fore- and hind limbs cannot yet be determined in any specimen, there is considerable indirect evidence suggesting that the forelimbs are longer than the hind limbs, but they are probably not as different in length as in Recent sea turtles.

The humerus is longer than the femur (fig. 67). Its shaft is slightly S-shaped in side view, and the axis of the caput humeri stands at an angle of about 140° to that of the shaft (fig. 68), about the same value obtained in *Eretmochelys*. The angle between the longitudinal axis of the shaft and the plane of movement (fig. 69) is about 29° , intermediate between those of *Chelydra* ($\pm 10^\circ$) and *Lepidochelys* ($\pm 68^\circ$). These two angles (figs. 68, 69) express most clearly the typical differences between humeri that are moved in a horizontal plane (as in fresh-water turtles) and those that move in a vertical plane (as in sea turtles). The transition from the former to the latter type involves (1) enlarging of angle α (fig. 68), which straightens the caput humeri in relation to the shaft, (2) an axial rotation of the entire humerus to the extent of something less than 90° , and (3) increase in the angle β (fig. 69), which produces a more anterior position of the distal end of the humerus relative to the caput humeri and therefore permits greater freedom of movement within the limits imposed by the shell. While angles α and β can be measured on any well-preserved humerus, the amount of axial rotation of this element with regard to the body as a whole can only be determined on Recent material. Angle α (fig. 68) of $\pm 90^\circ$ is primarily correlated with the retractability of the forelimb. Since the bridge of the shell in most fresh-water turtles, though not in chelydrids and trionychids, sets a limit to the extent to which the humerus can be pulled backward, angle α of $\pm 90^\circ$ extends the range of horizontal movability forward to the point where the elbow touches the neck (fig. 71). If angle α were significantly greater than 90° it would impair the retractability of the limb and would extend the range of movement farther outward and backward. An extended position such as is theoretically indicated in figure 71, right, is not seen, to my knowledge, in any fresh-water turtle, including those with reduced plastra where the axillary notch of the shell is more than adequate to permit that position.

In fresh-water turtles, angle β (fig. 69) determines the position of the elbow with regard to the plane of the plastron; it is above this plane if the angle is small ($\pm 10^\circ$ in *Chelydra*). A significantly greater angle would lower the elbow below the plastral plane, a theoretical position that could scarcely be considered functional (fig. 71).

In view of these functional considerations, we may be justified in regarding the values of angles α and β as indicative of the type of movement of the humerus in a fossil form even though the axial position of this element with regard to the body is not determinable. The values of α and β in the toxochelyid humerus suggest that it was moved in a vertical plane as in sea turtles and that the forelimb was not retractable. With regard to angle β , it is less specialized than in any

of the Recent cheloniids. This conclusion is supported by the position of the radial tuberosity distal to the caput humeri. In the Toxochelyidae, the radial tuberosity is a single, large process; in the Cheloniidae, it actually consists of two processes whose cartilage-covered ends are proximally connected and form an inverted "V." The distal joint surface of the toxochelyid humerus may have permitted greater mobility at the elbow than is possible in Cheloniidae, but much less than in the Chelydridae. According to Wieland's (1902) account of the forelimb of *Toxochelys*, the zeugopodial bones are of nearly equal length (the radius slightly longer than the ulna) and they lie side by side in the plane of the manus. My own observations on other materials confirm Wieland's account, except that one specimen (C.N.H.M. PR136, *T. moorevillensis*) indicates a somewhat longer radius, to judge from the length of the proximal and distal pieces of the left radius that do not fit together yet are together as long as the left ulna. Two well-preserved ulnae are available and neither shows a distal rugosity, indicating a contact with the radius. In this respect, the forelimb is chelydrid, not cheloniid. The few carpal elements available in the specimens at hand differ notably from those illustrated by Wieland. One of these elements (C.N.H.M. PR123, *T. latiremis*, fig. 70) compares well with the central carpal of *Chelonia*, and the other, very probably the product of fusion of two or three distal carpals, resembles somewhat the fused distal carpal element 3+4+5 in *Chelonia*. Since PR123 is a larger specimen than that illustrated by Wieland, the noted discrepancy probably reflects a difference in age of the two individuals. The carpus of Recent sea turtles attains its final state of ossification only in old individuals. According to Wieland, ulnare and intermedium are not elongated as in cheloniids. The manus is partially specialized in the direction of a sea-turtle flipper. The first and second digits are chelydrid and have large, curved, claw-bearing end phalanges (fig. 70). The remaining digits, particularly the third and fourth, are elongated. The elements illustrated in the position of the third digit in figure 70 are not necessarily correctly determined as such, but there is no reasonable doubt that they belong to the manus.

In summary, it may be said that comparative morphological and functional analysis suggests that the toxochelyid forelimb was a flipper moved in a vertical plane as in the cheloniids, but it was not as highly specialized as in that group.

The hind limb of *Toxochelys*, in contrast to the forelimb, is chelydrid throughout, with the possible exception of the tarsal elements, whose joint surfaces are somewhat more restricted than in *Chelydra* (fig. 70).

In *Toxochelys*, the major organs of propulsion of the sea turtles are thus combined with those of the fresh-water turtles. Functionally, this could mean that the Toxochelyidae could employ either the chelydrid or the cheloniid type of locomotion, using either the forelimbs or the hind limbs for steering. The chelydrid type of locomotion might have been used for quick escape, the cheloniid type for cruising. Phylogenetically, the Toxochelyidae represent a stage in the transition from a chelydrid to a cheloniid type of locomotion, in which the hind limbs are scarcely modified.

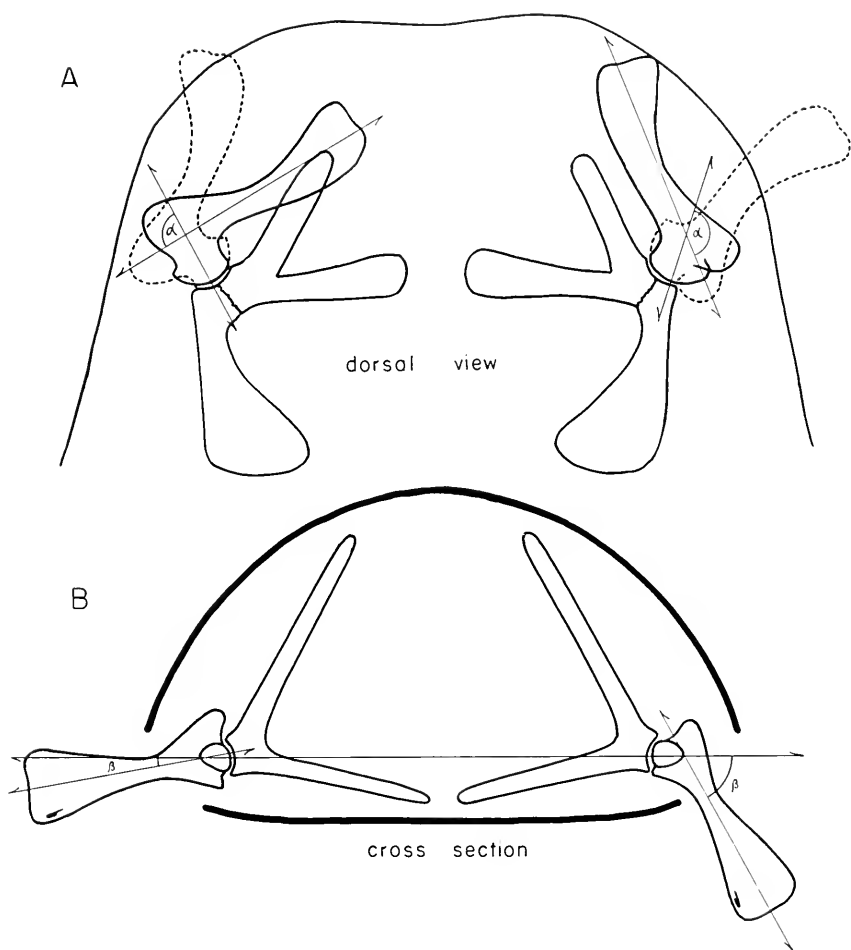


FIG. 71. A. Dorsal view of shell, shoulder girdle, and humerus to illustrate functional significance of angle α . B. Cross section view of shell, shoulder girdle, and humerus to illustrate functional significance of angle β . See page 169.

COMPARISON OF MORPHOLOGICAL AND FUNCTIONAL CHARACTERISTICS OF LIMBS IN FRESH-WATER TURTLES, SEA TURTLES, AND TOXOCHELYS

<i>Fresh-water turtles</i>	<i>Toxochelys</i>	<i>Sea turtles</i>
<i>All four legs used in swimming; hind limbs major organs of propulsion</i>		<i>Forelimbs major organs of propulsion; hind limbs used for steering</i>
1. Hind limbs longer than forelimbs	Forelimbs probably longer than hind limbs	Forelimbs much longer than hind limbs
2. Femur longer than humerus	Humerus longer than femur	Humerus longer than femur
<i>Forelimbs more in horizontal plane in swimming; retractable; also used for walking and digging</i>		<i>Forelimbs more in vertical plane; not retractable; cannot be used for walking or digging</i>
3. Humerus "S"-shaped	Humerus slightly "S"-shaped	Humerus nearly straight
4. Angle of head to shaft $\pm 90^\circ$	Angle of head to shaft $\pm 140^\circ$	Angle of head to shaft $\pm 127^\circ$ or more
5. Axis of shaft $\pm 10^\circ$ off plane of movement	Axis of shaft $\pm 29^\circ$ off plane of movement	Axis of shaft $\pm 68^\circ$ off plane of movement
6. Radial process at level of head	Radial process distal to caput humeri	Radial process distal to caput humeri
7. Distal joint surface strongly convex; extends to ventral side	Distal joint surface convex; extends to ventral face	Distal joint surface much restricted and relatively flat
8. Radius and ulna lie in plane of manus	Radius and ulna lie in plane of manus	Radius and ulna lie in a plane approximately rectangular to that of manus
9. Large spatium interosseum	Large spatium interosseum	Small spatium interosseum
10. Radius shorter than ulna	Radius slightly longer than ulna	Radius much longer than ulna
11. No contact rugosity between radius and ulna	No contact rugosity between radius and ulna	Contact rugosity between radius and ulna
12. Carpal elements almost spherical	Carpal elements flattened; joint surfaces restricted	Carpal elements flattened; joint surfaces restricted; ulnare and intermedium elongated
13. Digits 2, 3, and 4 normal in length	Digits 3 and 4 elongated	Digits 2, 3, and 4 greatly elongated
14. Claws on digits 1, 2, and 3	Claws on digits 1 and 2	A claw on first digit only
<i>Hind limbs major organs of propulsion; retractable; toes 4 and 5 can be spread to increase paddle surface</i>		<i>Hind limbs steering organs; not retractable</i>
15. Femoral trochanters separated by depression	Femoral trochanters separated by depression	Femoral trochanters connected
16. Distal joint surface of femur strongly convex	Distal joint surface of femur strongly convex	Distal joint surface of femur relatively restricted
17. Fibula with distal lateral ridge	Fibula with distal lateral ridge	Fibula without distal lateral ridge
18. Tarsal elements with joint surfaces reaching to dorsal face of tarsus	Tarsal elements intermediate between Chelydridae and Cheloniidae	Tarsal elements with flat joint surfaces
19. Claws on digits 1, 2, and 3	?	A claw on first digit only
20. Metatarsus V movable in lateral direction	Metatarsus V movable	Metatarsus V scarcely movable
21. Four phalanges on fifth digit	?	Three phalanges on fifth digit

REVISION OF THE FAMILY TOXOCHELYIDAE

Family TOXOCHELYIDAE

Characterization.—Extinct sea turtles. Skull with primary or secondary palate; temporal region partially roofed. Small nasal bones present or absent. Cervical vertebrae short, as in Cheloniidae. Forelimbs developed as primitive flippers; hind limbs chelydrid throughout. Carapace circular, oval, or, more rarely, cordiform. Neural plates flat or keeled, in continuous series. Epineurals only in keeled forms. Almost always fontanelles of varying size between costal and peripheral plates. A pair of small fontanelles at posterior end of nuchal plate, or conspicuous thinness of shell at that point. Two suprapygial plates. Vertebral shields in adult individuals always narrower than pleural shields. Plastron of cruciform shape with distance between axial and inguinal notches 60 per cent or less than half the width of the plastron. Late Cretaceous, North America.

The toxochelyid turtles readily fall into three groups: generalized, unkeeled forms with primary palates; unkeeled forms with secondary palates; and keeled forms with palates intermediate between the two types. These three groups will be recognized as subfamilies below.

Subfamily Toxochelyinae

Characterization.—Relatively generalized toxochelyid turtles. Skull with primary palate and narrow triturating surfaces anteriorly. Anterior vomer area wide and smooth. Triturating shelf of mandible at symphysis narrower than lower shelf. Small nasal bones. Carapace circular, rarely cordiform. Neuralia flat. Peripheral edge of carapace without serrations (see below). Moderate fontanelles between costal and marginal plates. Nuchal fontanelles in *Toxochelys* only. Plastron with small central and lateral fontanelles and, consequently, long hyo-hypoplastral suture. Xiphiplastra widest at mid-length, posteriorly tapering to a point. No elevations, or only faint ones, on hyo- and hypoplastra.

Toxochelys, Porthochelys, Thinochelys

Horizon and locality.—Late Cretaceous, North America.

Discussion.—Skulls are known only in the genera *Toxochelys* and *Porthochelys*. In both genera, the basic designs of the skull and mandible are very similar, and the differences are mostly of a quantitative nature. The skull of *Porthochelys* is much more robust and much wider than that of *Toxochelys*. Both strength of construction and over-all width are correlated with the size of the masticatory surface areas on upper and lower jaws.

The masticatory surfaces of upper and lower jaws in *Porthochelys* are widest near their posterior ends and involve notable portions of the palatines. An isolated mandibular ramus, here tentatively referred to *T. atlantica* (p. 196), is

	<i>Toxochelys latiremis</i> Y.P.M. 3604	<i>Porthochelys laticeps</i> , type K.U. (V.P.) 1204
a. Length of skull.....	115 mm.	111 mm.
b. Width of skull at posterior end of triturating surface.....	80 mm.	109 mm.
c. Posterior width of triturating surface.....	12 mm.	24 mm.
b \times 100 a =	69.6	98.2
c \times 100 a =	10.4	21.6

specialized as in *Porthochelys*. Small nasal bones are present in both genera. The vertebral column, the girdles and the limb-bones are discussed above.

The shells in the three genera are rather flat, circular, or broadly cordiform in outline and there are always at least small lateral fontanelles. There is no pit in the second peripherals for the antero-lateral prong of the hyoplastron. The carapace is unkeeled and the peripheral edge is even except in *Porthochelys*, where the peripherals are slightly serrated behind the marginal scale furrows, thus differing from the condition in lophochelyine forms where the serrations are always in front of the scale furrows.

The plastra in the three genera differ notably with regard to the relative degree of excavation of the axillary and inguinal notches and the length of the hyo-hyoplastral sutures:

	Axillary-inguinal distance mm.	Hyo-hyoplastral suture mm.	Index
<i>Toxochelys weeksi</i> U.T. K20	46.5	70	66.4
<i>Toxochelys barberi</i> C.N.H.M. P27047	35.0	65	53.8
<i>Toxochelys latiremis</i> (juv.)..... K.U. (V.P.) 1244	33.5	44	76.1
<i>Toxochelys latiremis</i> Y.P.M. 3602	24.0	44	54.5
<i>Toxochelys moorevillensis</i> C.N.H.M. P27330	42.0	\pm 76	55.2
<i>Toxochelys moorevillensis</i> C.N.H.M. P27348	46.0	68	67.6
<i>Porthochelys laticeps</i> K.U. (V.P.) 1204	53.0	\pm 59	89.8
<i>Thinochelys lapiosseae</i> C.N.H.M. P27453	41.5	86	48.2

Toxochelys Cope

Characterization.—Skull with narrow masticatory surfaces, not at all or only slightly involving palatine bones. Small nasal bones. Carapace oval or more or less circular, with moderate to extensive costo-peripheral fontanelles. A pair of post-nuchal fontanelles. Sutures between adjoining neural plates variable, but most often rounded as in *Thinochelys*. Greatest width of mid-dorsal neurals exceeds half their length. Greatest width of fourth neural contained fourteen to eighteen times in width of carapace. Postero-lateral peripherals (in

specimens with small fontanelles) about as wide as long. Suprapygial plates more or less equal in maximum width. Posterior width of second vertebral shield much more than half its length. Medial sulci of marginal shields not visible on peripheral plates, except sometimes on postero-lateral elements. Posterior edge of pygal plate not distinctly notched. Plastron with moderate central and lateral fontanelles. Width of hypoplastron at narrowest point slightly greater than corresponding dimension of hyoplastron. Medial edges of hyo- and hypoplastron serrated. Shortest axillo-inguinal distance greater than half the length of the hyo-hypoplastral suture (observed percentages 54 to 76). Greatest width of xiphiplastron at mid-length, or, more often, in posterior half of element.

Type of genus.—*Toxochelys latiremis* Cope.

Horizon and locality.—Niobrara Formation, Kansas.

Recognized additional species.—*T. moorerillensis* sp. nov.; Mooreville Chalk, Alabama. *T. barberi* Schmidt; Marlbrook Marl, Arkansas. *T. atlantica* sp. nov.; Greensand, New Jersey. *T. weeksi* Collins; Coon Creek Tongue, Ripley Formation, Tennessee. *T. browni* Hay; Pierre Shale, South Dakota and Wyoming. *T. sp.*; Taylor Marl, Texas.

Discussion.—*T. brachyrhina* Case (pl. 11) is based on a badly crushed skull of *T. latiremis*.¹ The type specimen of *T. serrifer* Cope (pl. 16) consists of some skull fragments, a lower jaw and two postero-lateral peripheral plates, the latter not now with the specimen. Considering the fact that the skull fragments and particularly the mandible are uncrushed, these parts are virtually indistinguishable from *T. latiremis*, but careful comparison revealed that the skull fragments belong to a skull of the size of Y.P.M. 3602, whereas the mandible belongs to a much smaller individual, probably about the size of C.N.H.M. UR4. There can be no reasonable doubt that the lower jaw and the skull parts belong to two individuals. Since the peripheral plates are serrated, and since there is no other member of the genus *Toxochelys* that possesses serrated peripheral bones, the suspicion arises that a third individual (probably a lophochelyine turtle) became mixed with this lot of bones before it was handed to Professor Cope for description. Of the remaining species of *Toxochelys* recognized by Hay (1908), only *T. latiremis* belongs to the flat-neuraled forms. All other species are keeled and referable to the new genus *Ctenochelys* (p. 227).

Once the nature of *T. latiremis* and its morphological relationship to the Mooreville material were recognized, it became evident that a number of undescribed specimens and several species described under different generic names from various formations belong to *Toxochelys*. Among the described species, *Phyllemys barberi* Schmidt (pl. 24) from the Marlbrook Marl of Arkansas, *Porthochelys browni* Hay (pl. 10) from the Pierre Shale of South Dakota, and the carapace (Y.P.M. 625) referred to *Lytoloma angusta* by Wieland (1904b) and to

¹ Dr. Edwin C. Galbreath, of the University of Kansas, has studied the type specimen independently and has arrived at the same conclusion.

Lyttoloma wielandi by Hay (1908) from the Greensand of New Jersey (fig. 79) clearly belong to *Toxochelys*. The latter specimen is the type of *T. atlantica* sp. nov. (p. 196). Among undescribed specimens, the United States National Museum possesses from the Taylor Marl of Texas a partial shell that is referable to *Toxochelys*. A superbly preserved plastron, associated with three posterior peripheral plates, was recently discovered by Dr. R. Lee Collins, of the University of Tennessee, in the Coon Creek Tongue of the Ripley Formation in Tennessee. This specimen also belongs to *Toxochelys*.

Skull and mandible.—There are a surprising number of *Toxochelys* skulls available for study. Most of these belong to *T. latiremis* and a smaller number to *T. browni*; two partial skulls and a mandible belong to *T. moorevillensis* and an isolated mandibular ramus was tentatively referred to *T. atlantica*. The remaining species of the genus are known from shells only. The comparison of the skulls of the above-mentioned species involves careful consideration of the mode of preservation, in order to avoid, if possible, the description of "Gesetzmässigkeiten" in the post-mortem changes rather than actual morphological differences between the species.

T. latiremis and *T. browni* are very similar and can easily be distinguished from *T. moorevillensis* by the shape of the mandible. In the latter species, the triturating surface of the lower jaw forms a sharp sagittal crest along the dorsal shelf of the symphysis. This ridge divides posteriorly and continues as a blunt elevation along the inner margins of the triturating surface. The latter forms a pronounced valley. In *T. latiremis* and *T. browni*, the sagittal ridge is faint or entirely absent. The lingual border of the triturating surface is lower than the alveolar ridge, often not clearly delimited, and the masticatory surface is much less concave in medio-lateral direction. The skulls of *T. latiremis* and *T. browni* are more difficult to distinguish, perhaps because of the generally poor state of preservation of the materials from the Pierre Shale. The skulls from this formation range in size from about 74 mm. to about 170 mm. in snout to occipital condyle length. The latter value was never observed in *T. latiremis*, where a skull length of about 120 mm. appears to be adult size. In some skulls, furthermore, the premaxillary region of *T. browni* is more pointed—beak-like—than in *T. latiremis*. There seems to be good reason to consider *T. browni* as a distinct species, even though the state of preservation renders detailed comparison difficult. The jaw fragment tentatively assigned to *T. atlantica* differs from all other known species of the genus by the relatively great posterior width of the triturating surface. It is similar to *Porthochelys* in the direction of jaw specialization.

Carapace and plastron.—The shell of *Toxochelys* is easily distinguished from that of any other known genus of the subfamily and it is the best known. In the Mooreville Chalk of Alabama, shell remains of *Toxochelys* are numerically the most common finds, and this may also be true in the Niobrara, where the great majority of the turtle skull materials belong to this genus and where unbiased collecting would probably produce more shell material than is now available.

TABLE 8.—MEASUREMENTS AND INDICES OF FORELIMB AND HIND LIMB BONES IN TOXOCHELYIDAE, CHELYDRIDAE, AND CHELONIIDAE

Species	Length of humerus	Index	Length of radius	Index	Length of ulna	Index	Length of femur	Index	Length of tibia	Index	Length of fibula	Index
Toxochelyidae												
<i>Toxochelys latiremis</i>	37.0	100	34.0	90.6	23.0	61.3
Y.P.M. 3602.....
C.N.H.M. PR123.....	130.0	100	65.0	50.0
<i>Toxochelys moorevillensis</i>
C.N.H.M. PR136.....	±120.0*	100	60.0	50.0	113.8†	94.8	77.0	64.1	75.5	62.9
Chelydridae												
<i>Chelydra serpentina</i>	76.0	100	45.0	59.2	47.0	61.8	84.0	110.5	66.0	86.8	64.0	84.2
Private specimen (No. 21)...	43.0	53.1	46.0	56.8	80.0	98.7	58.0	71.6	57.0	70.3
C.N.H.M. 22058.....	81.0	100
<i>Macrochelys temminckii</i>
C.N.H.M. 22059 (subadult)...	68.0	100	39.0	57.3	38.0	55.8	70.0	102.9	52.0	76.5	52.0	76.5
Cheloniidae												
<i>Eretmochelys imbricata</i>	79.0	100	48.0	60.7	42.0	53.1	56.0	70.9	43.0	54.4	41.0	53.1
C.N.H.M. 31009 (subadult)...
<i>Chelonia mydas</i>	213.0	100	140.0	65.7	110.0	51.6	160.0	75.1	131.0	61.5	122.0	57.2
C.N.H.M. 22066 (adult).....

* Calculated from available fragments compared to humerus of *T. latiremis*, PR123.

† Calculated; length of fragment 109.0 mm.

The shell of *Toxochelys* shows a high intraspecific variability, a matter of importance if isolated finds are to be properly identified. The wide range of variation of the shell of *T. moorevillensis* (pl. 23) probably exists also in other species of which only one individual is known at present. Additional specimens that might be found in the Greensand of New Jersey or the Marlbrook Marl of Arkansas may thus be expected to differ notably from the type specimens of the respective species.

Presently available materials show clearly that the plastra of the different species of *Toxochelys* are very similar but can be separated on the basis of differences in proportion, as indicated in Table 9.

The vertebral column, the girdles and limb-bones of *Toxochelys* were discussed at length above. Since these are unknown or poorly known in other genera of the family, valid generic comparisons are not yet possible.

TABLE 9.—PLASTRAL INDICES IN DIFFERENT SPECIES OF TOXOCHELYS

Species	A	B	C	D	E	F
<i>Toxochelys moorevillensis</i> , C.N.H.M. PR136...	±75.0	21.9	±78.3
<i>Toxochelys moorevillensis</i> , C.N.H.M. P27330...	73.0	15.4	22.1	9.6	74.5
<i>Toxochelys moorevillensis</i> , C.N.H.M. P27348...	69.7	16.5	24.3	13.4
<i>Toxochelys weeksi</i> , U.T. K20.....	64.8	17.7	21.9	16.8	65.4	87.3
<i>Toxochelys barberi</i> , C.N.H.M. P27047.....	67.7	16.5	22.0	16.5	64.2	102.4
<i>Toxochelys latiremis</i> , K.U. (V.P.) 1244 (juv.)...	55.0	18.7	20.6	23.7	66.9
<i>Toxochelys latiremis</i> , Y.P.M. 3602.....	59.2	21.4	18.2	19.5	64.9

A = length of hyo-hyoplastral suture

B = width of umbilical fontanelle

C = hypoplastron at narrowest point

D = width of lateral fontanelle

E = length of xiphiplastron

F = lateral expansion of hyoplastron

All indices except F were calculated as follows: value $\times 100$ /total width of hyoplastron

F was calculated as follows: value $\times 100$ /lateral expansion of hyoplastron

Toxochelys latiremis Cope

Toxochelys latiremis Cope, Proc. Acad. Nat. Sci. Phila., p. 10, 1873; Rept. U. S. Geol. Surv. Terr., 2, pp. 98, 260, pl. 8, figs. 1, 2, 1875; Proc. Amer. Phil. Soc., 17, p. 176, 1877; Hay, Field Columbian Mus., Zool., 1, p. 101, pls. 14, 15, 1896; U. S. Geol. Surv. Bull., 179, p. 442, 1902; Bull. Amer. Mus. Nat. Hist., 21, p. 177, 1905; Carnegie Inst. Wash. Publ., 75, p. 168, figs. 200, 202–206, 1908; Case, Univ. Kansas Geol. Surv., 4, p. 371, pl. 79, pl. 80, figs. 1, 2, pl. 81, figs. 1–8, 10–13, pl. 82, figs. 1–3, pl. 83, figs. 2–4, 1898; Wieland, Amer. Jour. Sci., (4), 14, p. 95, fig. 1, 1902.

Toxochelys brachyrhina Case, Univ. Kansas Geol. Surv., 4, p. 378, pl. 84, figs. 1, 2, 1898; Hay, U. S. Geol. Surv. Bull., 179, p. 442, 1902; Bull. Amer. Mus. Nat. Hist., 21, p. 177, 1905; Carnegie Inst. Wash. Publ., 75, p. 171, pl. 31, fig. 1, 1908.

Toxochelys serrifer Cope, Rept. U. S. Geol. Surv. Terr., 2, p. 299, 1875; Hay, U. S. Geol. Surv. Bull., 179, p. 442, 1902; Bull. Amer. Mus. Nat. Hist., 21, p. 178, figs. 1–7, 1905; Carnegie Inst. Wash. Publ., 75, p. 170, figs. 207–213, 1908.

Cynocercus incisus Leidy, Rept. U. S. Geol. Surv. Terr., 1, p. 269, pl. 36, figs. 17–21, 1873.

Type.—A.M.N.H. 2362, jaw fragment (pl. 15) and coracoid.

Horizon and locality.—Niobrara Formation. Near fork of Smoky Hill River, Kansas.

Referred specimens.—Two skulls (A.M.N.H. 1496 and 1497) were described and referred to this species by Cope (1877) and were figured by Hay (1908). Other skulls were described and figured by Hay and Case as cited. The following, mostly unpublished, skulls and mandibles were studied and identified as *T. latiremis*: Y.P.M. 3602, skull and partial shell; Y.P.M. 3609, skull and mandible; Y.P.M. 3604, skull and mandible; Y.P.M. 3611, skull, vertebrae, girdle-bones, epiplastron, and limb-bones; Y.P.M. 1386, partial skull; Y.P.M. 3610, mandible; Y.P.M. 1387, mandible; A.M.N.H. 5118, skull and mandible; A.M.N.H. 1497, skull and mandible (figured by Hay, 1908); A.M.N.H. 11875, partial skull; A.M.N.H. 1042, partial skull; A.M.N.H. 5119, mandible; A.M.N.H. 1498, mandible; A.M.N.H. 181, mandible; A.M.N.H. 5999, mandible; A.M.N.H. 1835, skull fragments and mandible (2 individuals) (=type of *T. serrifer*); U.S.N.M. 11560, skull; U.S.N.M. 11559, skull; U.S.N.M. 11639, partial skull; U.S.N.M. 1496, partial skull and mandible; U.S.N.M. 11558, partial skull; U.S.N.M. 12011, mandible; U.S.N.M. 12010, mandible; K.U. (V.P.) 1212, skull and mandible (=type of *T. brachyrhina*); K.U. (V.P.) 8352, mandible; K.U. (V.P.) 1210, mandible; K.U. (V.P.) 8256, mandible; C.N.H.M. PR125, fragmentary skull (juv.); C.N.H.M. UR9, fragmentary skull (juv.); C.N.H.M. UR4, mandible, vertebrae (juv.); C.N.H.M. UR3, mandible; C.N.H.M. PR124, mandible.

The shell of this species is represented by only three specimens, the most important of which is Y.P.M. 3602, because of its association with a good skull. The other shells are: C.N.H.M. PR123, partial carapace and plastron, girdle-bones, limb-bones, and vertebrae; K.U. (V.P.) 1244, partial carapace, good plastron, anterior part of skull, vertebrae, girdle-bones, and limb-bones (juv.).

Questionably referred specimens: Y.P.M. 3605, nuchal plate, first peripheral, epiplastron, humeri; K.U. (V.P.) 1291, isolated neural plate; U.S.N.M. 12007, epiplastron, first peripheral, other shell fragments, humerus, scapula; C.N.H.M. UR93, poorly preserved assemblage of miscellaneous bones on a slab.

Amended diagnosis.—Skull similar to that of *T. moorevillensis*, but mandible without sagittal ridge on triturating surface. Shell thin, circular in outline, with wide lateral fontanelles extending from the nuchal plate probably to the suprapygal area. Width of lateral fontanelles much greater than that of adjoining peripherals. Antero-lateral and postero-lateral peripherals not greatly different in width. Nuchal plate with small, pronounced ventral boss. Second and third vertebral shields much wider than long. Plastron considerably reduced medially and laterally (see Table 9).

Discussion.—Considering the number of specimens, the abundance of isolated skulls and mandibles is difficult to understand. It is true that the shell of *T. latiremis* is thin and delicate, but certainly no more so than the skull. While

I am not familiar with the circumstances of burial and preservation in the Niobrara deposits, I am hesitant to accept the above proportion of skulls to shells as the ratio at which these skeletal parts actually occur in the deposit. The suspicion arises that a bias in collecting was involved, since partial shells, broken into countless pieces, may well have been considered worthless specimens, whereas skulls, even when broken, were collected.

There is, of course, no way of knowing how many of the skulls were accompanied by elements of the post-cranial skeleton in the field. What evidence there is in this and other species from the Niobrara Chalk seems to indicate that skulls and shells usually occur dissociated, as is the rule in most other formations.

Skull and mandible.—At first sight, the skull material listed above presents a picture of apparently great variety. Not only are there broad and narrow skulls with pointed or blunt snouts, but there are enough qualitative differences between them to permit distinguishing each skull from all the others (pls. 10–13). Almost all materials show obvious signs of post-mortem distortion, particularly dorso-ventral crushing to various degrees of intensity, as evidenced by numerous breaks through the bones. This form of distortion produces differences in proportion, and, because it is plainly visible, causes few difficulties. But there are cases where the dorsal part of a skull, for example, is badly fractured and crushed, whereas the palate shows few and very minor fissures (pl. 12). Such apparently unchanged areas demand the exercise of caution. The differences between skulls in such areas may be real individual variations, but there is rarely proof of this, since bone, under formational pressure, may be altered in shape without external evidence of such change. It is thus impossible to separate entirely true morphological features from those brought about by the hazards of preservation. It is with the utmost caution that similarities and differences are treated in the following account.

The skull of *T. latiremis* is, on the whole, delicately constructed. It is much longer than wide, possibly of the general proportions of that of *Chelonina*. In their present condition, the width of all skulls is greatly exaggerated. It is even more difficult to arrive at a conclusion as to the original height of the skull of this species. Earlier students thought it had been much like that of *Chelydra*, but this view underestimates the severity of the flattening in the posterior half of the skull. The snout region may have been of the general relative height of that of *Chelydra*, but the posterior half was higher, perhaps as high as in Recent sea turtles. The cranial roof extends backward to approximately the junction of the pro-otic and opisthotic bones. It is thus farther excavated than in *Chelonina* or *Caretta* and much less so than in *Chelydra*. The orbits were slightly longer than high and faced outward and upward, to judge from the relative narrowness of the interorbital bridge. The shape of the external nasal opening was a character used to distinguish the species (Hay, 1908), but this is certainly not a reliable feature, since it is always injured by compression. It appears safe to state, however, that the opening was wider than high in life. In front of the

nasal opening, the premaxilla forms a triangular, flattened area, with the apex of the triangle facing the tip of the snout and the base forming a transversal crest that delimits the nasal opening anteriorly. The apex of this triangular area is separated from the alveolar edge of the premaxillae by a very short distance, about 2 mm. in the largest skulls. The typical pattern of the dorsal skull bones is illustrated in figure 60. Distinct, small nasal bones are definitely determinable in U.S.N.M. 1496.

The ventral aspect shows a number of differences between the skulls that may, possibly, be interpreted as individual variations. In Y.P.M. 3604, the anterior vomer area is concave and laterally confluent with the triturating surfaces of the maxillae. In A.M.N.H. 5118, the vomer area is separated from the triturating surfaces by a pronounced, sharp crest that continues backward along the palato-maxillary suture. Intermediate conditions with either blunt crests or sharp crests not reaching forward to the vomer area are seen in Y.P.M. 3602, 3609, and others. In Y.P.M. 3602, the ventral surface of the pterygoids is subdivided into three areas by two curved, longitudinal ridges that follow approximately the lateral edges of the pterygoids. In most of the specimens, these ridges are less pronounced and in Y.P.M. 3604 they are but faintly visible. It may also be noted that there is considerable variation in the size of the palatine vacuities.

The mandibles show many recognizable differences, but, again, distortion may in part be responsible. Most mandibles are somewhat flattened in dorso-ventral direction, resulting in similar over-all preservation but in differences in proportion between the masticatory shelf and the chin-shelf at the symphysis. The length of the chin-shelf appears to be nearly always exaggerated. In the apparently undistorted mandible associated with the type specimen of *T. serrifer* (A.M.N.H. 1835), the chin-shelf extends downward and not as far backward as in most specimens. C.N.H.M. UR4, of about the same size as A.M.N.H. 1835, is so severely crushed that the chin-shelf lies almost at the level of the triturating surface and mostly behind it. Notable differences in the antero-posterior curvature of the mandibular rami may also be due to differences in preservation. In the better-preserved specimens, the mandible is rather acutely pointed. There is a faint sagittal ridge on the triturating surface. The suture pattern of the mandible is illustrated in figure 60.

Vertebral column.—Save for the atlas, the cervical region of the vertebral column is documented by a complete series of relatively well-preserved vertebrae in PR123 (pl. 20, A). As has been noted in the general discussion above, the cervical region in *Toxochelys latiremis* is shorter than in *Chelonia* and *Chelydra* (see fig. 62). The centra of vertebrae 2, 3, 4, and 5 are approximately circular in cross section (disregarding the large ventral keel projection); those of numbers 6 and 7 are flat and wide and the centrum of number 8 is wide anteriorly, more or less circular behind. The pattern of central articulation is

$$(2), (3), (4), (5), (6), (7), (8).$$

The double facet between centra 7 and 8 may be an individual variant, rather than the typical condition of this species (see general discussion). The neurapophyses are connected by well-developed pre- and postzygapophyses and a spinal process occurs only on the second vertebra. Neurapophyses 2-5 have pronounced, paired muscle pits on the dorso-medial sides of the postzygapophyses; neither in *Chelydra* nor in *Chelonia* are there pits of equal depth and sharpness of definition, and on the second vertebra such pits are absent. The postzygapophyses of vertebrae 6-8 are sharply crested dorsally. In vertebrae 6 and 7, these crests converge anteriorly and meet near the anterior ends of the neurapophyses. In the eighth cervical, the crests ascend to form the surface resting against the ventral knob of the nuchal plate. The transverse processes are similar to those of *Chelonia*, and much more pronounced than in *Chelydra*. Associated with PR123 is the first shell vertebra, the centrum of which is very strongly keeled ventrally. The spinal process of its neurapophysis appears to have been free from the carapace; it is much expanded at its end. The centrum of the third or fourth shell vertebra is without ventral keel. The three sacral vertebrae, with their ribs in place, are preserved in Y.P.M. 3602. The neurapophyses show clearly that this region was not fused with the shell. The sacral ribs increase in size from the first to the third and they are distally in firm contact.

Carapace and plastron.—Entire shells of this species are not yet known and our knowledge of the carapace, in particular, still leaves much to be desired. The available materials suggest that the carapace is flat and is circular or broadly oval in outline. Continuous lateral fontanelles extend from the nuchal to the suprapygal or even the pygal. The fontanelles are about as wide as the lateral dimensions of the adjoining costal plates. The peripherals are notably longer than wide. There is a pair of large post-nuchal fontanelles.

The nuchal plate (fig. 73) is wider than long and moderately excavated along its cervical border. In C.N.H.M. PR123 (fig. 72), it is straight in front, but this is due to crushing. On the ventral side of the nuchal, there is a conspicuous boss, no doubt homologous to the similar but much larger protuberance in cheloniid, dermochelyid, and protostegid turtles. In Y.P.M. 3605 and C.N.H.M. UR93, tentatively referred to this species, the nuchal appears to have a different shape. Y.P.M. 3605 was figured by Wieland (1905, p. 337). Examination of the specimen left some doubt as to the outline of the postero-lateral edges of the plate; these may have been trimmed somewhat during preparation. C.N.H.M. UR93 has a very severely crushed nuchal that resembles Y.P.M. 3605 in some respects, but its postero-lateral and lateral edges are not satisfactorily preserved. Severe crushing may account for the apparent differences in shape between these nuchals and those in other specimens, but there is one difference that cannot be explained by post-mortem changes, namely, the size of the ventral boss. In C.N.H.M. UR93, it is very much smaller than in C.N.H.M. PR123.

There is no complete neural series in any specimen. The preserved elements indicate that the series was essentially as in *T. moorevillensis*. The first costal

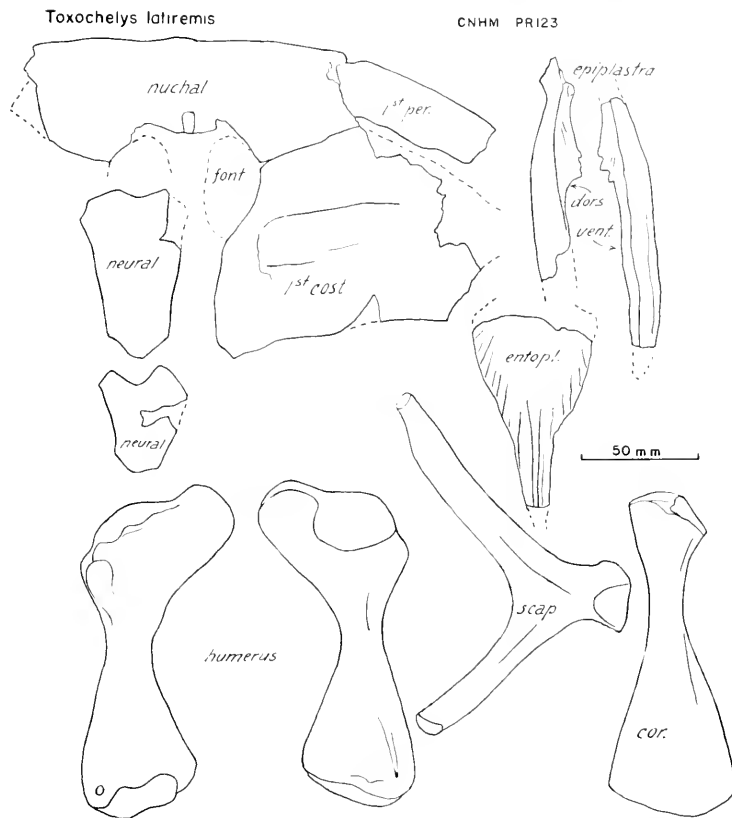


FIG. 72. Outline drawing of some important parts of specimen of *Toxochelys latiremis* (C.N.H.M. PR123).

plate is much wider in antero-posterior direction than the following costals (fig. 73). The lower suprapygal and the pygal are unknown.

In the posterior part of the carapace, the width of the peripherals amounts to about 60–70 per cent of their length in Y.P.M. 3602. In the juvenile K.U. (V.P.) 1244, as expected, the peripherals are much narrower, the width being about 30–40 per cent of their length. The marginal edges of the peripherals are faintly notched at the shield furrows. The vertebral shields are much wider than long, more so than in *T. atlantica* and in notable contrast to those of *T. moorevillensis* and *T. barberi*, where the third vertebral shield, for instance, is as long as wide.

The plastron of *T. latiremis* is better known than the carapace. In K.U. (V.P.) 1244, the plastron is preserved largely *in situ* (fig. 73 and pl. 21) and is complete except for the entoplastron. The juvenile proportions of the plastral

parts differ notably from those of Y.P.M. 3602. The central and lateral fontanelles are larger in this species than in any of the others and the plates are thin (see Table 9). Furthermore, the hyo- and hypoplastra are shorter across the narrowest points and the xiphiplastra are more slender than in the other species of the genus. The epiplastra (fig. 72) have an enlarged anterior end with a sharp process on the dorsal side. Behind this point, the elements are constricted. A thin, bony flange faces the entoplastron (fig. 72). In K.U. (V.P.) 1244, this flange had probably not yet developed. Along the posterior half of the medial border, the epiplastra adhere to the hyoplastron. The area of contact is clearly marked on both elements by rugosities. An epiplastron associated with the skull of Y.P.M. 3611 resembles those of C.N.H.M. PR123 described above, except for the lack of the medial flange. Epiplastra are, furthermore, associated with Y.P.M. 3605 (figured by Wieland, 1905) and with U.S.N.M. 12007, both specimens doubtfully referred to this species. There is probably a good deal of variation in detail among the epiplastra of different individuals and those described here are probably not characteristic of this species.

In C.N.H.M. PR123, most of the entoplastron is preserved (fig. 72). It is a thin, more or less triangular plate with a sagittal ridge on the posterior half of the dorsal surface. This ridge becomes gradually broader and blunter and ceases to be an elevation at the anterior, broken end of the plate. The ventral face of the entoplastron is flat.

Shoulder girdle and limbs.—The right scapula and left coracoid (C.N.H.M. PR123) are complete but somewhat crushed (fig. 72). The glenoidal region of the scapula is slightly heavier than in *Lepidochelys* and the angle formed by the glenoidal and coracoidal facets is but little larger than 90° , as in *Chelydra*; in *Lepidochelys* and other cheloniids, it is in the vicinity of 150° . The shape of the coracoid is very much like that of *Lepidochelys*. The proportions of the different shoulder girdle elements are discussed on page 162.

A fair portion of the pelvis, both ilia, the right ischium, and a very incomplete pubis are associated with Y.P.M. 3602. I can see no differences between these bones and their homologues in *T. moorevillensis*.

Besides the limb-bones described by Wieland (1902), only one other specimen with associated limb-bones has come to my attention. This is C.N.H.M. PR123. Both humeri and ulnae, a proximal fragment of a radius, some carpal bones, metacarpi and digits I and II, and other elements of II and/or IV are preserved (fig. 70). None of the bones of the hind limbs are present. Most of these limb-bones are well preserved and not unduly crushed. A general description of these bones was given in the discussion of the toxochelyid limb. In addition to the elements of the manus mentioned and figured (fig. 70) above, there are nine partial bones of the hand, none of which can be pieced together. Their position in the hand cannot be determined. In so far as comparison with the forelimb of *T. moorevillensis* is possible, I cannot detect any differences other than those of preservation.

Toxochelys latiremis

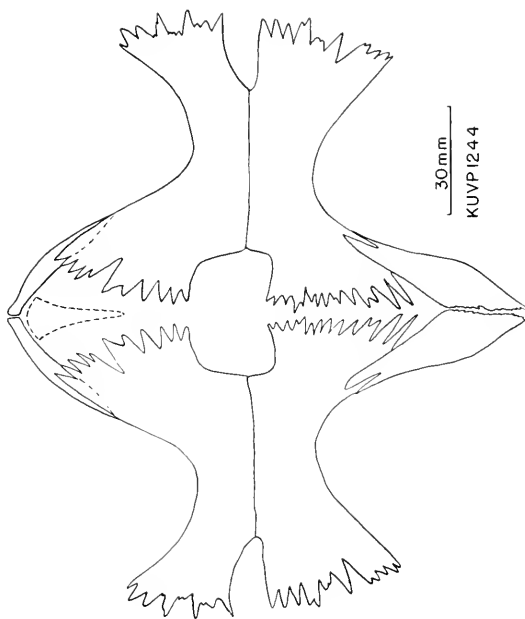
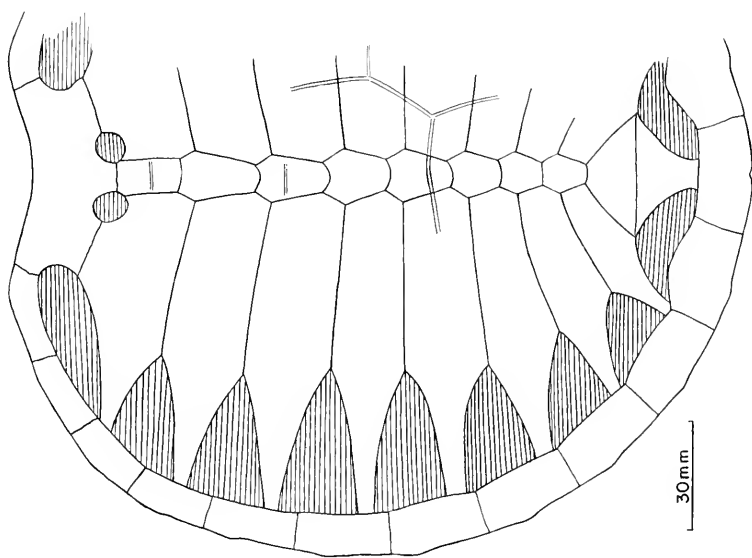


FIG. 73. Reconstruction of carapace and plastron of juvenile specimen of *Toxochelys latiremis*.

Of the hind limb of *T. latiremis*, only the femur is definitely known (Y.P.M. 3602), and it compares, in every respect, very closely with that of *T. moorevillensis*. Y.P.M. 3602 is the only specimen of the genus in which the relative length of humerus to femur can be determined.

***Toxochelys moorevillensis* sp. nov.**

Type.—C.N.H.M. P27330, a nearly complete shell, vertebral fragments and girdle bones.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Moore Brothers farm, Harrell Station area, Dallas County, Alabama.

Referred specimens.—Eutaw area, Greene County, Alabama: C.N.H.M. PR168, costal plates; C.N.H.M. P27434, fragmentary specimen; C.N.H.M. PR32, fragmentary specimen; C.N.H.M. P27348, partial carapace and plastron; C.N.H.M. P27438, peripherals; C.N.H.M. P27444, peripherals.

Burkville area, Lowndes County, Alabama: C.N.H.M. PR136, nearly complete shell, girdle bones, some limb-bones, and some vertebrae (locality: SW. $\frac{1}{4}$ SW. $\frac{1}{4}$ NW. $\frac{1}{4}$ sec. 33, T. 16 N., R. 16 E.); C.N.H.M. PR218, mandible (locality: NE. $\frac{1}{4}$ NE. $\frac{1}{4}$ NE. $\frac{1}{4}$ sec. 5, T. 15 N., R. 16 E.).

Clinton area, Greene County, Alabama: C.N.H.M. PR113, fragment.

Harrell Station area, Dallas County, Alabama: C.N.H.M. P27391, a nearly complete carapace, fragments of plastron, vertebrae, and a good pelvis; C.N.H.M. PR110, fragmentary specimen; C.N.H.M. PR224, shell fragments; C.N.H.M. PR188, fragmentary specimen; C.N.H.M. P27367, fragmentary plastron; C.N.H.M. PR191, fragmentary plastron; C.N.H.M. PR189, fragmentary plastron; C.N.H.M. PR199, anterior part of carapace; C.N.H.M. PR109, fragmentary specimen; C.N.H.M. PR264, peripherals; C.N.H.M. PR265, costal plate; C.N.H.M. P27358, peripherals; C.N.H.M. P27549, fragmentary specimen; C.N.H.M. P27347, fragmentary plastron; C.N.H.M. P27554, fragmentary specimen; C.N.H.M. P27562, costal plate; C.N.H.M. P27556, fragmentary specimen; C.N.H.M. P27555, fragmentary specimen; C.N.H.M. PR266, peripherals; C.N.H.M. P27349, fragmentary specimen; C.N.H.M. P27544, costal plate; C.N.H.M. P27436, peripheral fragments; C.N.H.M. P27539, peripheral fragments; C.N.H.M. P27345, costal plate; C.N.H.M. PR194, neural and costal plates; C.N.H.M. P27550, partial skeleton; C.N.H.M. PR140, peripherals; C.N.H.M. PR144, partial carapace; C.N.H.M. PR219, skull (good braincase); C.N.H.M. P27338, posterior portion of skull.

Cedarville area, Hale County, Alabama: C.N.H.M. P27346, fragmentary specimen (locality: T. 11, west of Highway 13).

West Greene area, Greene County, Alabama: C.N.H.M. PR167, nearly complete shell and pelvis (locality: 1.6 miles north and $\frac{1}{2}$ mile west of West Greene); C.N.H.M. PR155, carapace fragments; C.N.H.M. PR154, fragmentary specimen; C.N.H.M. PR253, peripherals; C.N.H.M. PR166, partial carapace.

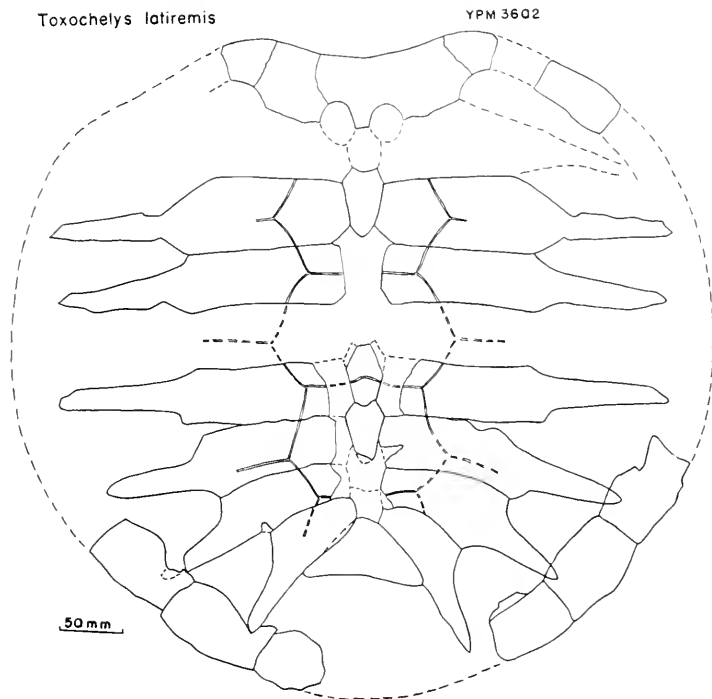


FIG. 74. Carapace of *Toxochelys latiremis* (Y.P.M. 3602). Associated with this shell is the skull illustrated on plate 10.

Mt. Hebron area, Greene County, Alabama: C.N.H.M. PR28, nearly complete carapace and several vertebrae (locality: $\frac{1}{2}$ mile north of Mt. Hebron); C.N.H.M. PR26, peripherals.

Boligee area, Greene County Alabama: C.N.H.M. PR111, fragmentary specimen; C.N.H.M. PR112, fragmentary specimen; C.N.H.M. PR60, costal plates; C.N.H.M. PR33, fragmentary specimen; C.N.H.M. PR59, anterior peripherals.

Diagnosis.—Skull as far as known similar to that of *T. latiremis*. Mandible with sharp sagittal crest on triturating surface, dividing the latter into right and left halves. Triturating surface concave on either side of ridge. Carapace circular, with continuous lateral fontanelles of moderate size and variable extent, usually from second to eleventh peripherals. Smallest observed fontanelles extending from posterior end of third to anterior end of ninth peripherals. Fontanelle opposite eleventh peripheral (if present) always small, not significantly affecting suprapygal plates. Postero-lateral fontanelles always narrower than adjoining peripherals. Antero-lateral peripherals much narrower than postero-lateral peripherals. Plastron relatively primitive with small umbilical and lateral fontanelles, and long xiphiplastr (see Table 9).

TABLE 10.—MEASUREMENTS AND INDICES IN THE PELVIS OF
TOXOCHELYS MOOREVILLENSIS

Specimen number	<i>Pubis</i>		<i>B</i>		<i>C</i>	
	<i>A</i>					
	mm.	Index	mm.	Index	mm.	Index
C.N.H.M. P27391	49.0	100	30.0	61.2	18.0	36.7
C.N.H.M. PR167	34.0	100	26.0	76.4	18.0	52.9
C.N.H.M. P27330	43.0	100	35.0	81.4	19.5	45.3
C.N.H.M. PR166	36.5	100	23.5	64.4	21.5	58.9
<i>Ischium</i>						
C.N.H.M. P27391	49.0	100	47.0	95.5	14.0	28.5
C.N.H.M. P27550	40.0	100	11.0	27.5
<i>Ilium</i>						
C.N.H.M. P27391	58.0	100	47.0	81.0	16.0	27.5
C.N.H.M. PR167	44.0	100	34.0	77.3	11.0	25.0
C.N.H.M. P27330	50.0	100	49.5	99.0	14.5	29.0
C.N.H.M. P27550	52.5	100	48.0	91.4	14.0	26.6
C.N.H.M. P27554	53.0	100	46.0	86.7	15.0	28.3
C.N.H.M. PR136	58.0	100	46.0	79.3	14.5	25.0

Pubis A = width of plate from middle of symphyseal edge to lateral edge.

B = width of symphyseal process of pubis at its base (narrowest point).

C = width of antero-lateral process of pubis.

Ischium A = maximal transversal extent of bone.

B = length of posterior process measured from its end to anterior edge of ischium.

C = width of ischium at narrowest point lateral to posterior process.

Ilium A = maximal dorso-ventral height of ilium.

B = length of dorsal process, measured from its posterior end to antero-dorsal face of shaft.

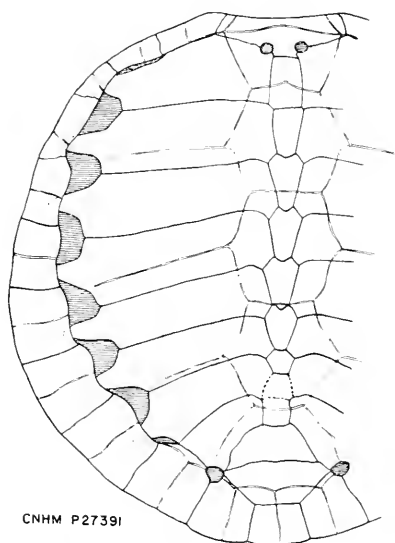
C = antero-posterior diameter of shaft at narrowest point (about mid-height).

Description.—Among about sixty specimens collected, only three skulls and one mandible were secured. In view of the fact that, as a matter of policy, *all* fossil remains were picked up, this ratio reflects the actual occurrence of the skulls and shells in the field and probably in the formation. These figures are particularly interesting if compared with the number of shells and skulls of *T. latiremis* preserved in the collections (see p. 179).

The two partial skulls (C.N.H.M. P27338 and C.N.H.M. PR219) and the mandible (C.N.H.M. PR218) were found isolated (pl. 14). Although there are some differences between these materials and those of *T. latiremis*, the similarity leaves no doubt that they belong to the Mooreville species of the genus *Toxochelys*. The skulls are smaller than the largest skulls of *T. latiremis*. Specimen P27338 corresponds in size approximately to *T. latiremis* Y.P.M. 3602; PR219 and the mandible are slightly larger and compare with *T. latiremis* Y.P.M. 3609 (pl. 14).

Unfortunately, the skulls are too incompletely preserved to permit close comparison with *T. latiremis*, but in so far as comparison is possible, no significant differences can be observed. The braincase of PR219 is excellent and is described and compared with *Chelonia* and *Chelydra* (see p. 150 and pl. 9).

The mandible (PR218), on the other hand, is provided with a sharp ridge along the symphyseal line of the triturating surface, the latter being thus divided

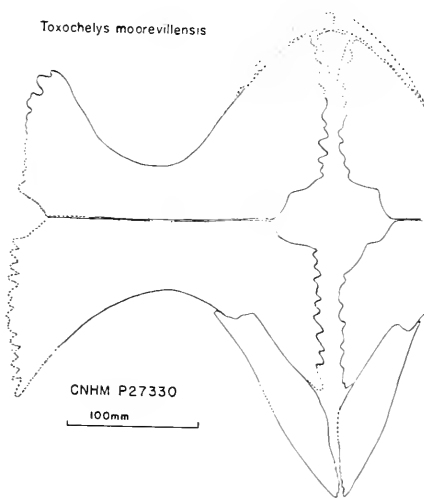


CNHM P27391

Toxochelys moorevillensis

100mm

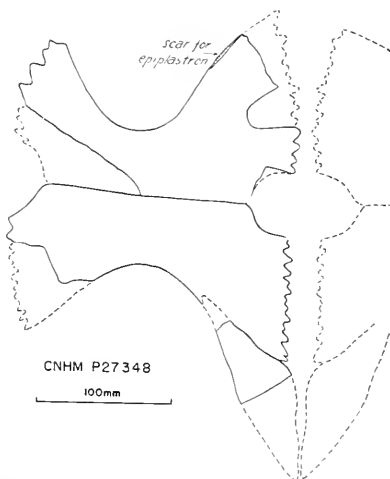
FIG. 75. Carapace of *Toxochelys moorevillensis*.



Toxochelys moorevillensis

CNHM P27330

100mm



scar for
epipastron

CNHM P27348

100mm

FIG. 76. Plastra of *Toxochelys moorevillensis*. The plastron of P27330 is the more typical of the two.

into right and left portions. The sagittal ridge divides posteriorly and is continued as a rounded swelling along the lingual margins of the triturating surfaces (pl. 14). The latter are thus clearly delimited medially and are rather deeply concave transversely. The mandible of *T. moorevillensis* is easily distinguishable in all of the described features from that of *T. latiremis*, where there is none or only a faint symphyseal crest, where there is no sharp medial delimitation of the triturating surfaces, and where the latter are only slightly concave in medio-lateral direction.

Vertebral column.—Considering the large number of specimens, only a few vertebrae are available. The best are associated with P27391 (pl. 20). Of the cervicals, the centrum of the seventh lacks an unmistakable double joint surface posteriorly. The neural canal is much wider, even between the attachment scars of the neural arches, than in the sixth centrum of *Ctenochelys tenuitesta* and there is but a faint sagittal ridge at the base of the neural canal. The eighth cervical vertebra lacks most of the dorsal extent of the neurapophysis and the right prezygapophysis. This is a most remarkable vertebra, since it bears perfectly discrete, short, conical ribs, the apices of which face backward (pl. 20). The centrum is very short and broad (Table 3). A single centrum of an anterior shell vertebra is definitely unkeeled ventrally. The few shell vertebrae directly preceding the sacral series, the (?)second sacral, and the anterior caudal vertebrae of this specimen have been discussed (see p. 157 and pl. 20). The only other vertebrae of *T. moorevillensis* are two caudals (PR136) belonging probably to the middle section of the tail. These vertebrae correspond rather closely with those of *C. tenuitesta*, except for the apparent lack of haemapophyses. In place of such elements, there are paired ventral processes of the centrum (pl. 20).

Carapace and plastron.—The shell of *T. moorevillensis* is rather well known. A number of specimens are complete enough to permit reconstruction of the shells (pls. 22 and 23).

The carapace is quite flat and almost circular in outline, at least in the fossil condition. The bones are thin compared to the size of adult individuals; anterior costal plates of such specimens are about 3–4 mm. thick in uncrushed condition. In crushed condition, the thickness may be reduced to half. The pattern of the carapace plates consists of a nuchal, nine neurals, two suprapygals, a pygal, and on either side eight costals and eleven peripherals. Occasionally, there is a ninth pair of costal plates (as in P27330, pl. 22) or there are nine costals on one side and eight on the other (as in P27391, pl. 23). The relative frequency of occurrence of this irregularity must be high in this species, since two out of three shells (P27391, P27330, PR136) in which this area of the shell is known show the abnormality. The eighth costal is not preserved in any other specimen, so that the relative frequency of occurrence cannot yet be determined. A comparable abnormality is seen in *Chelydra serpentina*, where it was seen once in eight individuals inspected. As a rule, lateral fontanelles extend from the third (in PR28 from the first) peripheral to the eleventh, but occasionally they are small and extend only from the fourth to the anterior half of the eighth (pls. 22

and 23), in which case costals 6 to 8 are suturally attached to peripherals 8 to 11. The degree of fontanellization is apparently independent of size, since PR136 and P27330 are of nearly equal size. Individuals PR167 and PR28 are much smaller than P27330 and P27391, yet their fontanelles are not much larger than in the fully grown specimens. In juvenile individuals, however, a notable difference should be expected, since the costal disk grows laterad in all turtles. There is a considerable difference in the width between the antero-lateral and postero-lateral peripherals (pls. 22 and 23). This is not the case in species with larger fontanelles (e.g. *T. barberi* or *T. latiremis*). The process of fontanellization affects not only the distal ends of the costal plates, but also the medial edges of the peripherals. This is evident if individuals PR136 and PR167 are compared. In the former, the ninth peripheral is as wide as long, in the latter it is much longer than wide (pl. 23). The medial margins of the dorsal faces of the peripherals are notably scalloped in *T. moorevillensis*. The vertebral shields, particularly the second, third, and fourth, are approximately equal in length and width, but there is a specimen (P27330, pl. 22) where they are much wider than long, as in *T. atlantica* and in *T. latiremis*. The plastron varies in detail individually, as does the carapace. On the whole, the posterior lobe is narrow and sharply pointed (pl. 22), but P27348 (fig. 76) has a plastron resembling that of *T. barberi* (fig. 77). The epiplastra are represented by fragments only; they are very narrow, delicate bones of the approximate shape indicated in figure 76. The entoplastron is absent in all specimens. Hyo- and hypoplastra have slight ventral elevations at the corresponding places where keel bosses are present in the lophochelyine members of the family. The general proportions of the plastron are given in Table 9.

Girdles and limbs.—Associated with PR136 is a nearly complete left half of the shoulder girdle with the scapula and coracoid preserved *in situ*. The dorsal process of the scapula is relatively shorter than in *T. latiremis* (Table 5). The coracoid is much more expanded posteriorly than in *T. latiremis*, where the narrowest part of the coracoid is contained 3.6 times in the posterior width; in *T. moorevillensis* (PR136), the comparable value is 4.8.

Pelvic elements are relatively well represented in the present material. Save for the left ilium, a well-preserved pelvis (fig. 65) is associated with P27391. Partial pelves are available in PR167, PR166 (fig. 65), PR136, P27550, P27554, P27330 and P27349. As pointed out above (p. 161), there is a notable amount of individual variation in the dimensions of the pubes and ilia (see Table 10). The pubes of PR167 fit together perfectly along their symphyseal borders, indicating an original bone-to-bone contact as in the Chelydridae, rather than a partial separation by a cartilage sheet as in the Cheloniidae. The symphyseal border of the pubis, gradually increasing in thickness, swings outward anteriorly where it probably supported a prepubic cartilage.

The forelimb of this species is documented by rather meager materials. There is not a single complete humerus preserved with any of the numerous shell specimens, but there is at least one isolated humerus that probably belongs to

T. moorevillensis (e.g. P27403, illustrated in fig. 69). Associated with PR136 are the distal halves of both humeri, the left ulna, the proximal two-thirds of the left radius and the distal ends of both radii. The foot-bones preserved with this specimen very probably belong to the pes. A fragment of a proximal humerus is associated with P27554. All of these elements show very little crushing and have

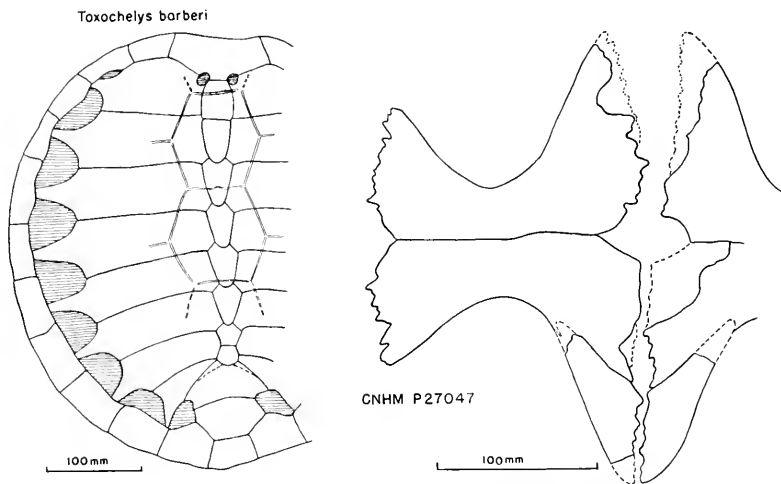


FIG. 77. Carapace and plastron of *Toxochelys barberi*.

good surface detail. The radius of this species may be relatively longer than in *T. latiremis*, but the evidence is not entirely conclusive. The two radial fragments mentioned are together about as long as the ulna, but the cross sections at their broken ends are very different; a portion of about 4-5 mm. may be missing.

The hind limb of *T. moorevillensis* is better documented than the flipper. Proximal and distal femur fragments are associated with PR136, PR110 and P27349 (fig. 70). The head of the femur is displaced far to the tibial side (ventral in the articulated position of the femur to the pelvis) and the tibial trochanter is directly behind it (fig. 70). The fibular trochanter is relatively much more massive than in *Chelydra*. The positional relationship of the trochanters to the head is illustrated in figure 70. The distal end of the femur is very strongly convex; the joint surface reaches from the dorsal side of the bone to the ventral side, and there can be no doubt but that there was great movability at the knee joint.

In PR136, both tibiae and the right fibula are complete; the left fibula is represented by proximal and distal fragments (fig. 70). There is a notable similarity between these elements and their homologues in *Chelydra*. The fibula, in particular, has a flaring, thin ridge at its distal, lateral edge, essentially as in *Chelydra*. The distal end of the tibia bears two joint facets, separated by a

saddle-shaped depression. In *Chelydra*, there is an indication of such a separation, but in *Chelonia* there is none. The large proximal tarsal element (a product of the fusion of tibiale + intermedium + fibulare + centrale) is very well preserved (fig. 70). It belongs to the left side and has clearly marked joint facets facing the zeugopodial bones and another for the enlarged distal tarsal 4 + 5. The tibial joint surface consists of two facets that are separated by a "V"-shaped depression. The fibular joint surface is transversely elongated (fig. 70). The joint surfaces between this large proximal element and the distal tarsal 4 + 5 are much more clearly defined than in *Chelydra* and in general resemble the condition in an old specimen of *Chelonia*, except that the joint permits a somewhat greater range of movement than in the latter form.

The proximal end of metatarsus V has a rather extensive joint surface corresponding to a complementary surface on distal tarsal 4 + 5. There is, on metatarsus V, a small additional joint facet for at least a partial articulation of metatarsus IV, much as in *Chelydra* and *Chelonia*. No doubt the fifth metatarsal was movable, as in *Chelydra*, and both digits IV and V could be spread as in fresh-water turtles (fig. 70).

There are two additional tarsal elements whose position I cannot determine with certainty. Most of the phalanges are broken and their position in the pes is doubtful. One of these, an entire element, is believed to be the ground phalanx of digit V. The other elements are tentatively identified as metatarsal fragments, and if this is correct, have distinctly chelydrid character.

Toxochelys barberi (Schmidt)

Phyllemys barberi Schmidt, Field Mus. Nat. Hist., Geol. Ser., 8, p. 65, figs. 20-22, 1944.

Type.—C.N.H.M. P27047, a mounted shell with part of the posterior costal area restored.

Horizon and locality.—Marlbrook Marl, Late Cretaceous. Cox farm, one mile northeast of junction of Hollywood-Okolona road to Arkadelphia, Clark County, Arkansas.

Amended diagnosis.—Carapace circular, with continuous lateral fontanelles from the second to the eleventh peripherals. Lateral areas of suprapygal plates reduced. Postero-lateral fontanelles about as wide as the adjoining peripherals. Degree of fontanellization intermediate between *T. moorevillensis* and *T. latiremis*. Vertebral shields 2 and 3 about as long as wide. Plastron similar to that of *T. weeksi*, but with lateral expansion of hyoplastron greater than that of hypoplastron and with medial expansion of hyoplastron smaller in area than in *T. weeksi*.

Discussion.—The type is the only known specimen. When it was re-examined a pair of post-nuchal fontanelles were found, though these were filled with plaster in the mount. The peculiarities of the shell pattern at the proximal ends of the eighth costal plates, as reconstructed, were not necessarily there in life; the area is too incompletely preserved, however, to permit a definite conclusion. At any rate, the matter is of little concern, since irregularities of this sort are

known in Recent turtles. In the plastron, the xiphiplastra, in particular, had to be remounted.

The great similarity of this specimen to members of the genus *Toxochelys*, as here understood, is unmistakable.

The carapace of this species (pl. 24) shows clearly a more advanced stage of aquatic specialization than that of *T. moorevillensis* (fig. 75). The lateral fontanelles are larger, particularly in the posterior part of the shell where the suprapygals, reduced laterally, adjoin the fontanelles for a notable distance (fig. 77), and where the peripherals are considerably longer than wide. In the degree of fontanellization, *T. barberi* is probably intermediate between *T. moorevillensis* and *T. latiremis*, though more material of *T. barberi* is necessary to determine the amount and the trend of variation in this form. It cannot be satisfactorily determined whether eight or nine neurals are present. As in the typical specimens of *T. moorevillensis* (fig. 75), vertebral shields 2 and 3 are about as long as wide.

The plastron (pl. 24; fig. 77) is not as acutely pointed posteriorly as in *T. latiremis* and *T. moorevillensis*, and the xiphiplastra are relatively wider at mid-length than in the compared species. The lateral expansions of hyo- and hypoplastra are of nearly equal width, thus differing from the similar plastron of *T. weeksi*, where the hypoplastron is much wider laterally than the hypoplastron. For the general proportions of the plastron, see Table 9 and the discussion of *T. weeksi* below.

***Toxochelys weeksi* Collins**

Toxochelys weeksi Collins, Journ. Tenn. Acad. Sci., **26**, (4), pp. 262-269, 2 pls., 1951.

Type.—U.T. K20, Collins collection, a beautifully preserved partial plastron and three postero-lateral peripherals.

Horizon and locality.—Coon Creek Tongue of Ripley Formation, Late Cretaceous. Dave Weeks place, Coon Creek, McNairy County, Tennessee.

Dr. R. Lee Collins, of the University of Tennessee, who collected the specimen, kindly furnished me with excellent casts of the bones.

Diagnosis.¹—Peripheral plates 8, 9, and 10 suggest a carapace with lateral fontanelles. Plastron similar to that of *T. barberi*, but with relatively greater surface area of medial expansion of hypoplastron and with lateral expansion of hypoplastron smaller than that of hypoplastron. Umbilical fontanelle relatively larger than in *T. barberi*.

Discussion.—The specimen (fig. 78) resembles the plastron of *T. barberi* more closely than that of any other species of the genus. There are a number of differences in proportion between the two forms, the most obvious of them being the lateral expansion of the hyo- and hypoplastra (see Table 9). The surface area of the medial expansion of the hypoplastron is considerably larger in *T. weeksi* than in *T. barberi*. The following figures may illustrate some of these pro-

¹ This species was described and placed in the genus *Toxochelys* by Dr. Collins on my advice. The task of diagnosing the species was left for the present revision.

portional differences. If the hyoplastron of *T. barberi* (which is preserved in a flattened condition but is not otherwise crushed) is slightly bent into its original shape, its width is the same as that of the undistorted hyoplastron of *T. weeksi*. Both measure 185 mm. between the tips of the lateral and medial prongs. The



FIG. 78. Plastron of *Toxochelys weeksi*. Drawn from cast of type specimen.

width of the hyoplastron at the narrowest point is 39 mm. in *T. weeksi*, 35 mm. in *T. barberi*. The distance between the medial end of the hyo-hyoplastral suture and the posterior end of the epiplastral suture scar (on the antero-lateral edge of the hyoplastron) is 88 mm. in *T. weeksi*, but only 78 mm. in *T. barberi*. The degree of fontanellization of the plastron of *T. weeksi* is greater than in *T. barberi*, as is evident by comparison of the length of the hyo-hyoplastral suture; it is 115 mm. in *T. weeksi*, but 138 mm. in *T. barberi*. These values indicate two modes of plastral reduction: in *T. barberi*, the plastral bones are reduced in size so that the plastron as a whole covers a smaller area of the ventral surface of the animal than in *T. weeksi*. In the latter, the plastral reduction manifests itself in the large size of the umbilical fontanelle.

Toxochelys atlantica sp. nov.

Lytoloma angusta Wieland, not Cope (in part), Amer. Journ. Sci., **18**, p. 187, fig. 3, pls. 6-8, 1904.

Lytoloma wielandi Hay (in part), Carnegie Inst. Wash. Publ., **75**, p. 157, text figs. 196-197, 1908.

Type.—Y.P.M. 625, carapace.

Horizon and locality.—Greensand. Barnesboro, Gloucester County, New Jersey.

Tentatively referred specimen.—Y.P.M. 728, fragment of left side of mandible.

Diagnosis.—Mandible with masticatory surface wider posteriorly than anteriorly, as in *Porthochelys laticeps*. Carapace oval and greatly fontanellized. Pygal-suprapygal connection nearly severed by right and left fontanelles. Anteriorly, fontanelles extend to nuchal plate. Antero-lateral peripherals very narrow. Pygal longer than wide. Vertebral shields much wider than long.

Discussion.—The mandible (Y.P.M. 728) is an isolated find, provisionally referred to this species because of its similarity to toxochelyine jaws. The specimen lacks most of the triturating surface near the symphysis, but the chin-shelf shows the symphyseal suture. The fragment of this left ramus extends back to about the posterior end of the triturating surface. The postero-lateral face of the bone is severely injured, showing a pick mark.

This specimen, like much of the material from the Greensand of New Jersey, is entirely uncrushed and presents excellent surface detail. The general configuration of the masticatory surface relative to the chin-shelf resembles strikingly that of *Porthochelys laticeps*. As in the latter species, the triturating surface is much broader posteriorly than anteriorly. It is concave in medio-lateral direction, except near the symphysis, and its medial boundary is clearly delimited as in *Porthochelys* and in *T. moorevillensis*. In the anterior half, the medial masticatory ridge is smooth, not rough as in *Porthochelys*, and in the posterior half it is sharp. Seen from the medial side, the inner masticatory ridge is peculiarly flat and rather sharply delimited against the mandibular sulcus (sulcus cartilaginis meckelii) (pl. 15, figs. 1 and 2).

To date, there is no evidence from bones of the shell that *Porthochelys* occurs anywhere but in the Niobrara beds of Kansas, and it would be unwise to postulate its occurrence in New Jersey on the basis of this fragment, since increase in the width of the masticatory surface is a feature of turtle organization that has evolved independently many times in the history of the group. Until proved otherwise, it would seem much more reasonable to assume that *T. atlantica* possessed a skull and jaws specialized similarly to those of *Porthochelys laticeps*.

The carapace is oval and characterized by a degree of fontanellization intermediate between *T. barberi* and *T. latiremis*. The lower suprapygal is posteriorly reduced to such an extent that its sutural contact with the pygal is nearly broken. Anteriorly, the fontanelles probably reached the nuchal plate; the nuchal and the anterior peripherals are not known. The pygal plate, in contrast to all other

species of the genus, is longer than wide. Peripherals 4 and 5 are very narrow compared to the postero-lateral peripherals, much more so than in *T. latiremis* or *T. barberi*.

The vertebral shields (fig. 79) are considerably wider than long, but less so than in *T. latiremis*. The plastron is unknown.

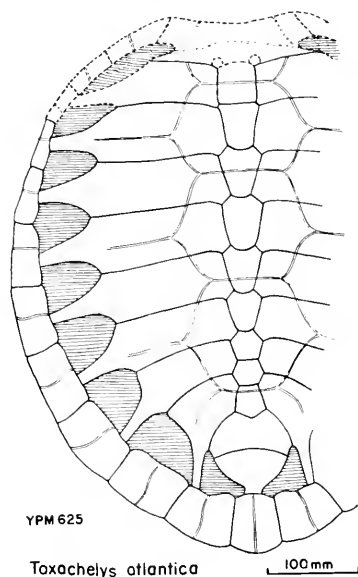
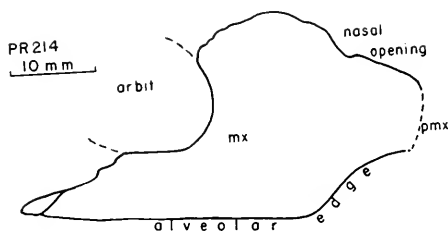


FIG. 79. Carapace of *Toxochelys atlantica*. After illustrations by Wieland.



Toxochelys browni

FIG. 80. Side view of snout region of skull of *Toxochelys browni*. *mx*, maxilla; *pmx*, premaxilla.

Toxochelys browni (Hay)

Toxochelys latiremis Wagner, Kansas Univ. Quart., 7A, p. 201, fig. 1, 1898.

Porthochelys browni Hay, Bull. Amer. Mus. Nat. Hist., 21, p. 183, figs. 15-16, 1905; Carnegie Inst. Wash. Publ., 75, p. 182, figs. 235-237, 1908.

Type.—A.M.N.H. 6080, large skull and mandible.

Horizon and locality.—Pierre Shale. Twenty miles southeast of Edgemont, South Dakota.

Referred specimens.—A.M.N.H. 5843, large skull and attached mandible; A.M.N.H. 1773, snout of medium-sized individual; A.M.N.H. 1774, small skull and mandible; A.M.N.H., unnumbered mandible; C.N.H.M. PR214, snout of medium-sized individual; C.N.H.M. PR213, skull and mandible of medium-sized individual; S.D.S.M. 425, large skull and mandible; S.D.S.M. 4610, large skull; K.U. (V.P.) 1221, partial skull; K.U. (V.P.) 1222, partial mandible.

Amended diagnosis.—Skull similar to that in *T. latiremis*, but premaxillary area more pointed and set off from maxillary region. Species considerably larger than *T. latiremis*. Shell unknown.

Discussion.—Nearly all of the material is badly preserved and not well suited for detailed description and comparison. Disregarding the size of the largest skulls, there is little ground for separating this form from *T. latiremis*. However, it may well be that the poor state of preservation obscured actual differences between the two forms. There are at least indications to this effect. Several of the skulls, including the type, seem to have a more slender premaxillary region, more or less distinctly set off from the maxillary region. This is seen in the large as well as in the small skulls, particularly along the alveolar ridge, where the latter appears slightly and broadly notched in the area directly behind the premaxillary-maxillary suture (pl. 10; fig. 80). This feature is most conspicuous in S.D.S.M. 4610, less so in S.D.S.M. 425. The squamosal has no forward extension as figured by Hay (1908, fig. 235, right side); as nearly as can be determined, it is exactly as in *T. latiremis*. The ventral aspect of the type skull appears to be devoid of ridges along the medial margins of the triturating surfaces and on the pterygoids, possibly because of bad preservation, since the bone surface is generally injured by adhering minerals. The mandible is indistinguishable from that of *T. latiremis*, except for the size range.

There can be no doubt that this form belongs to *Toxochelys* rather than to *Porthochelys*, and its closest known relative is *T. latiremis*. The fact that the size range greatly exceeds that of *T. latiremis*, together with indications of other differences, would seem to justify the retention of *T. browni* as a species distinct from *T. latiremis*.

Measurements: Length from Tip of Snout to Occipital Condyle

<i>T. browni</i>	mm.	<i>T. latiremis</i> (largest skull)	mm.
A.M.N.H. 6080.....	± 160	A.M.N.H. 5118.....	120
A.M.N.H. 5843.....	± 160		
S.D.S.M. 425.....	174		
S.D.S.M. 4610.....	173		
C.N.H.M. PR213.....	± 95		
A.M.N.H. 1774.....	± 75		

Toxochelys sp.

The United States National Museum preserves a fragmentary turtle specimen (U.S.N.M. 11797) that was collected by C. H. Kinzey in 1928, near Farmersville, Collin County, Texas, from the Taylor Marl, probably near the upper contact of this formation.

The specimen consists of a nuchal plate, three neurals, six partial costals, the first and third right peripherals, a mid-lateral peripheral, some fragments of the plastron, a proximal half of a femur, and some girdle fragments.

These materials unquestionably belong to a species of *Toxochelys*, but there is not quite enough evidence to determine whether it belongs to one of the described species or represents a new one. Under these circumstances, it would seem reasonable to refrain from making a decision in either direction at this time.

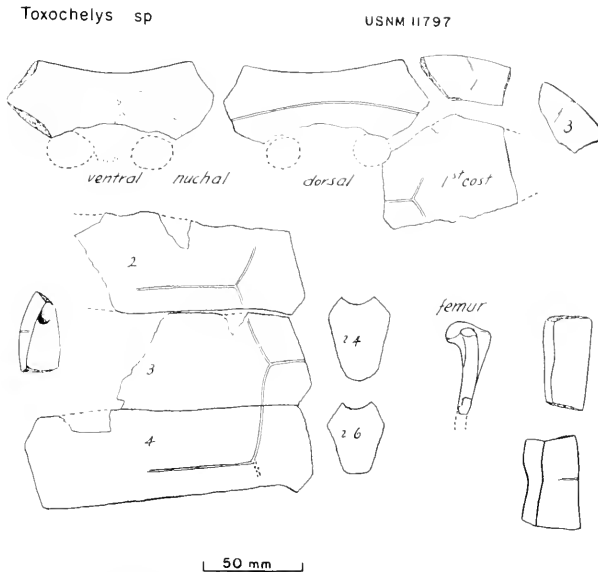


FIG. 81. *Toxochelys* sp. U.S.N.M. 11797, from Taylor Marl of Texas.

The nuchal plate resembles closely that of *T. barberi* (fig. 81). The anterior furrow of the first vertebral shield traverses the plate just posterior to its lateral corners. On the ventral side, there is a slight medial elevation as in *T. moorevillensis*, in place of a distinct knob as developed in *T. latiremis*. On the right side of the plate, the sharp edge bordering the post-nuchal fontanelle is preserved (fig. 81). The lateral fontanelles reach forward almost to the nuchal plate. The inner margin of the first peripheral is rather acute and without suture, except for a distance of about 5 mm. adjoining the nuchal. The degree of fontanellization anteriorly is thus greater than in *T. barberi* but not as great as in *T. latiremis*. The right third peripheral is of typical *Toxochelys* type, with the rib-pit at the extreme anterior end and with a very short ventral face. The neural plates are very slightly arched from side to side as is usual in *Toxochelys*, and the suture line between adjoining neurals is curved as in all species of *Toxochelys*. The second vertebral shield is about as wide as long.¹ The plastral fragments and that of the femur are clearly toxochelyid in form.

***Thinochelys* gen. nov.**

Characterization.—Skull unknown. Carapace ovate, widest at level of second costal plates, tapering toward pygal. Costo-peripheral fontanelles very

¹ This statement depends upon the correctness of my interpretation of the costal plates with regard to their position in the carapace.

small, discontinuous. No post-nuchal fontanelles. Adjoining neurals meet with sharply rounded sutures. Mid-dorsal neural plates about half as wide as long. Greatest width of fourth neural contained 21 times in width of carapace (measured over curvature). Postero-lateral peripherals longer than wide. Upper suprapygals much narrower than lower suprapygals. Posterior width of second vertebral shield half its length. Medial sulci of marginal shields visible on all peripheral plates. Posterior edge of pygal plate notched. Plastron with small central and lateral fontanelles. Width of hypoplastron at narrowest point about the same as corresponding dimension in hyoplastron. Medial edges of hyo- and hypoplastra only slightly serrated. Shortest axillo-inguinal distance half the length of hyo-hypoplastral suture (48 per cent). Greatest width of xiphiplastron in anterior half of element.

Type of genus.—*T. lapisossea*.

Horizon and locality.—Mooreville Chalk, Selma Formation. Alabama.

***Thinochelys lapisossea* sp. nov.**

Type.—C.N.H.M. P27453, well-preserved, nearly complete carapace, partial plastron and some vertebrae and girdle fragments.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Harrell Station area, one mile east of Harrell Station, south of railroad tracks, Dallas County, Alabama.

Referred specimens.—Harrell Station Area, Dallas County, Alabama: C.N.H.M. PR27332, a few peripheral bones and distal half of humerus; C.N.H.M. PR263, fragmentary carapace of large individual; C.N.H.M. PR201, both xiphiplastra.

Diagnosis.—As for the genus.

Description.—The bones of all three of the large specimens of this species have a bluish, opaline appearance and appear to be relatively heavier than those of most other turtles from the Mooreville Chalk of Alabama. Microscopic examination revealed that the bones are impregnated with calcite, as is the rule in bones from the Mooreville Chalk, and the bone cavities are entirely uncrushed in the microscopic section. This may be the reason why these bones are relatively heavy for their size.

Thinochelys lapisossea is a large, flat-neuraled toxochelyid. It has a heart-shaped carapacial outline and is rather highly arched. The degree of fontanelization of the carapace is nearly identical with that of *Porthochelys laticeps*; only small, irregularly shaped fontanelles exist between costal and peripheral plates from the second to the eighth costal. Between the fontanelles, the costal and peripheral plates are suturally united (pl. 25 and fig. 82).

The shortness of the nuchal plate in the photograph (pl. 25) is due to the curvature of the shell; actually, it is very similar in shape and proportion to that of *Toxochelys moorevillensis*. As in the latter form, the cervical edge of the nuchal is moderately excavated, more so than in figure 82. On the ventral side, the

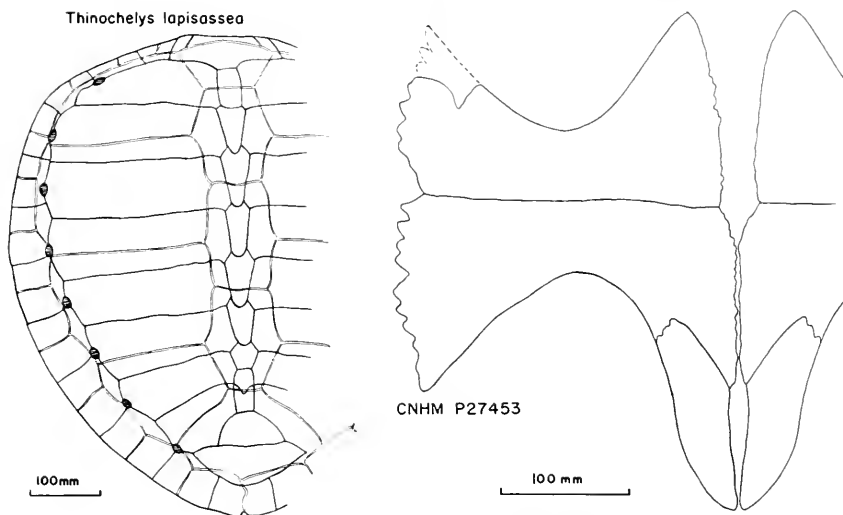


FIG. 82. Carapace and plastron of *Thinochelys lapisossea*.

nuchal shows a sagittal crest in its posterior half and there may or may not have been an anchor knob for the neural spine of the eighth cervical vertebra. The neural plates, nine in number as in *Toxochelys*, are narrow and elongated. The upper suprapygal is much smaller than the lower suprapygal. In *Thinochelys* and *Porthochelys*, the pygal is conspicuously notched at the shield furrow. The anterior two peripherals are very narrow. In peripherals 3 to 8 the dorsal face is very much longer than the ventral face. The bridge portion of the plastron was loosely connected to peripherals 4 to 8. In the type specimen, there is a pit, anterior to the rib-pit, in the eighth peripheral, which received the posterior-most lateral prong of the hypoplastron. A similar pit for the foremost lateral prong of the hyoplastron could not be found, but the width of the bridge area of the plastron suggests that it was near the anterior end of the fourth peripheral. In P27453, there are no smaller pits along the ventral edges of the bridge peripherals corresponding to the smaller lateral prongs of the plastron, but such pits are present in the larger PR263. The posterior peripherals are much longer than wide, in contrast to those in *Porthochelys*, which are much wider than long.

The scale pattern of the carapace is typically toxochelyid. The nuchal scale is short and wide, much as in the genus *Toxochelys*. The vertebral shields 2, 3, and 4 are much longer than wide. The inner shield furrows of all the marginal shields are visible on the peripheral plates, as in *Porthochelys*.

The shape of the plastron, except for the epi- and entoplastron, can be determined satisfactorily. Hyo- and hypoplastra are united by a long suture, so that neither the central nor the lateral fontanelles are as large as in *Toxochelys* or

Porthochelys. Compared to the last-named genus, the axillo-inguinal distance is relatively shorter, and the xiphiplastra are shorter and less pointed (fig. 82). The shield pattern cannot be determined.

A few posterior shell vertebrae and an anterior caudal are present in P27453. They are poorly preserved, however. Fragments of both shoulder girdle and pelvis are associated with the type specimen. The glenoidal ends of the right scapula and coracoid are intact. It is possible that the scapular contribution to the surface of the glenoidal cavity compared to that of the coracoid is a little greater in this species than in *Toxochelys*. The right ilium is attached to the acetabular ends of the pubis and ischium. It is very similar to that of *Toxochelys moorevillensis*. The posterior process of the ischium is exactly like that of *T. moorevillensis*.

Seen as a whole, there are a number of similarities in the shells of *Thinochelys* and *Porthochelys* and there are likewise differences. The two forms correspond with each other in the similar relative degree of fontanellization of the carapace, similar elongated shape of the anterior neural plates and the second vertebral shield, in the position of the medial shield furrows of the marginal scutes on the peripherals, and in the presence of a marked notch in the pygal at the scale sulcus.

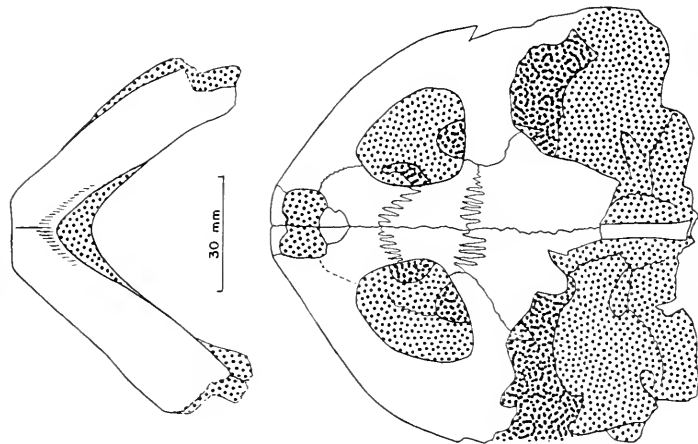
The two forms differ notably in the general shape and curvature of the shells, in the proportions of the peripherals, in the relative sizes of the two suprapygals plates, and in the degree of specialization of the plastron.

It is difficult to evaluate this situation taxonomically. I have chosen to regard the Alabama species as representing a genus different from *Porthochelys* rather than belonging to it, because differences between species of the same genus in other toxochelyid turtles are of a much lower order of magnitude than they are between the forms under discussion. This is also true among species of the same genus in Recent turtles.

Porthochelys Williston

Characterization.—Skull very broad, massive. Masticatory surfaces broader posteriorly than anteriorly. Carapace circular. Costo-peripheral fontanelles small, discontinuous; none lateral to the first costal plates. No post-nuchal fontanelles. Adjoining neurals meet with straight transverse sutures. Neurals long and narrow, but adjoining elements seem to differ greatly in length. Greatest width of fourth neural (estimated) contained about 18 times in width of the carapace. Postero-lateral peripherals wider than long. Suprapygals of about equal width. Posterior width of second vertebral shield about half its length. Medial sulci of marginal shields visible on all peripheral plates. Posterior edge of pygal plate notched. Plastron with moderate central and lateral fontanelles. Width of hypoplastron at narrowest point slightly smaller than corresponding dimension of hyoplastron. Medial edges of hyo- and hypoplastra serrated. Shortest axillo-inguinal distance about 90 per cent of length of hyo-hypoplastral suture. Greatest width of xiphiplastron in anterior half of element.

Porthochelys laticeps



Porthochelys laticeps

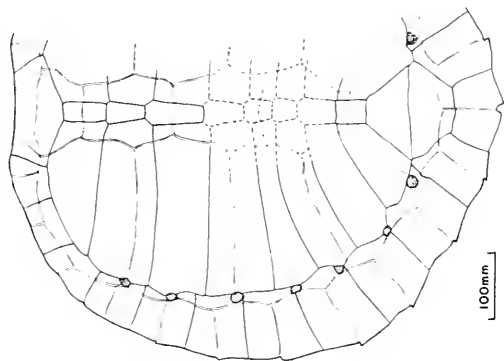


FIG. 84. Carapace and plastron of *Porthochelys laticeps*. After Williston.

FIG. 83. Skull and mandible of *Porthochelys laticeps*. Corrected illustration after Williston.

Type of genus.—*P. laticeps* Williston.

Horizon and locality.—Niobrara Formation. Kansas.

Porthochelys laticeps Williston

Porthochelys laticeps Williston, Trans. Kansas Acad. Sci., **17B**, p. 195, pls. 19-22, 1901; Hay, Bull. Amer. Mus. Nat. Hist., **21**, p. 183, 1905; Carnegie Inst. Wash. Publ., **75**, p. 180, pl. 31, figs. 2-3, text figs. 231-234, 1908.

Type.—K.U. (V.P.) 1204, shell, skull, mandible, and humerus.

Horizon and locality.—Niobrara Formation, Late Cretaceous. Kansas.

Amended diagnosis.—As for the genus.

Discussion.—Other than the type specimen, no additional material was discovered in the various collections that I studied. The genus has not been identified from any other formation and is absent in the Mooreville Chalk of Alabama, the fauna of which is otherwise similar to that of the Niobrara. All evidence indicates that *P. laticeps* is a rare find. The form may not have lived in the Niobrara sea, but rather in the adjacent coastal fresh water, and it may have become buried only occasionally in the chalk.

The skull is relatively short and broad and of heavy construction. It is dorso-ventrally crushed, however, and its width is somewhat exaggerated (fig. 83). The masticatory surfaces increase in width from front to back and their inner margins are distinctly serrated. The choanal and palatine openings are very large. The small nasal bones are easily visible in this specimen. The frontal bones are connected with the prefrontals and parietals by means of deeply inter-fingering sutures (fig. 83). The mandible is blunt in front. There is a slight sagittal ridge on the masticatory surface. The inner border of the latter is rugose anteriorly, smooth in the posterior two-thirds. In over-all appearance, the mandible resembles very much an isolated fragment, here tentatively referred to *Toxochelys atlantica* (pl. 15, figs. 1 and 2). There is no way of telling whether the latter was blunt or pointed in front; if my interpretation of a convergence in this case is correct, we may, on the basis of morphotypic predictability, assume that it was pointed. There are minor differences between these jaws. The triturating surface of *T. atlantica* is more deeply concave than that of *Porthochelys laticeps* and its inner margin is smooth in front rather than rough as in *P. laticeps*. There might well be other differences that could only be noted in side by side comparison of the specimens. While the general similarity is striking, it is not greater than that of the jaws of *Osteopygis* to those in the Recent genus *Caretta*.

The carapace is circular in outline, in preserved condition as wide as it is long. The costal disk is flanked by an unusually wide series of peripherals that are suturally connected with the costal plates, save for small fontanelles as in *Thinochelys*. In *Porthochelys* there is, however, no fontanelle lateral to the first costal. The anterior neural plates and the vertebral shields are similar in proportions to those of *Thinochelys*. Both suprapyrgals are equally wide. The medial shield furrows of the marginal scutes lie on the peripherals throughout, and the pygal is notched at the shield furrow. The peripherals show a slightly

serrated marginal edge. The serrations are located behind the shield furrows, not in front of them as in the Lophochelyinae. Nothing comparable is seen in *Thinochelys*.

The plastron has a relatively short hyo-hyoplastral suture and therefore rather large umbilical and lateral fontanelles. The xiphiplastra are long and relatively more pointed than in *Thinochelys* (fig. 84).

The humerus (Williston, 1901) should be difficult to distinguish from that of *Torocheilus*.

Subfamily Osteopyginae

Characterization.—Toxochelyid turtles with relatively generalized shells, and skulls provided with extensive secondary palates. Symphysis of mandible probably more than one-third the length of the ramus. Probably no nasal bones. Carapace oval, with or without small lateral fontanelles. Neuralia unkeeled. Peripheral edge of carapace not, or only slightly, serrated. A deep pit in the postero-medial face of the second peripheral plate for the reception of the antero-lateral prong of the hyoplastron.

Osteopygis, (?)Rhetecheilus

Discussion.—The type of specialization revealed by the fragmentary skulls and jaws in the Osteopyginae is very similar to that in the Cheloniidae, particularly the Recent genus *Caretta*, and some of the Early Cenozoic sea turtles of western Europe. If it were not for the definite association of one of the lower jaws with shell material of *Osteopygis* (A.M.N.H. 2216), there would be no reason for doubting the cheloniid affinities of these cranial materials. Accordingly, earlier students have placed various lots of these bones in different genera and families. Comparison of all available specimens reveals a moderately wide range of individual variation in the relative length of the mandibular symphysis, as well as some qualitative differences, such as a slight, blunt elevation on the triturating surface along the symphysis, or lack of such, as follows:

	Width between mental foramina mm.	Index	Length of symphysis mm.	Angle between canals alveolares	Elevation of symphysis
A.M.N.H. 2216.....	87	72	±63	55°	none
Y.P.M. 913.....	61	70.5	±43	50°	slight
Y.P.M. 602.....	68	76	52 (est.)	58°	slight
Y.P.M. 1001.....	74	78	58 (est.)	54°	slight
Y.P.M. 490.....	75	73	55	62°	medium
Y.P.M. 3613a.....	53	79	41 (est.)	53°	very slight
Y.P.M. 3613b.....	pronounced
<i>Erquelinnesia molaria</i> , type.....	88	74	65	±57°	none

The differences noted are quite insignificant, if viewed in the light of the unquestionably great over-all similarity of the specimens (pl. 16), and I propose, therefore, to include all of the skull and jaw materials listed above in the genus *Osteopygis*. The skull has a relatively broad and short snout region and an almost flat palate, thus differing from that of *Rhetechelys*, in which the snout is somewhat elongated and there is a pit behind the alveolar ridge of the premaxillae, presumably for the reception of an upturned mandibular beak.

The shell of *Osteopygis* is thick and spongy; the carapacial outline is oval and the degree of fontanelization varies greatly with the individual. Specimens without fontanelles are known. The lateral expansion of the hyoplastron reached forward to the second peripheral. The plastral shields are essentially as in *Toxochelys*.

The shoulder girdle is not satisfactorily known. The pelvis was described and illustrated by Wieland (1904a). Examination of these bones reveals rather too great an amount of modeling clay used in the reconstruction of the bones. Better material is necessary to determine the accurate shape of the pelvis.

Several humeri are known. The best one is associated with the type specimen of *Osteopygis gibbi* (Y.P.M. 783), and there is, with it, a left ulna. These elements are unmistakably toxochelyid in character, and such minor differences as seem to exist may be merely differences in preservation. This conclusion is based on the comparison of the humerus (Y.P.M. 778) with the humeral fragment of *Toxochelys moorevillensis* (P27554). These two specimens are entirely uncrushed and have good surface detail. As nearly as I can determine, the corresponding areas are practically identical. Comparison of the ulna of Y.P.M. 783 with that of *Toxochelys latiremis* (PR123) or *T. moorevillensis* (PR136) and *Chelydra* reveals that it is more chelydrid than in *Toxochelys*. In both genera, there is a sharp ridge along the outer edge of the ulna. Along the opposite edge, facing the radius, there are pronounced tuberosities proximally and distally in *Osteopygis* (fig. 90), indications of which are seen in *Chelydra*. In *Toxochelys*, there is, instead, a continuous sharp ridge.

The femur (Y.P.M. 783) is very much like that of *Toxochelys* (see Wieland, 1904a, fig. 6; Hay, 1908, fig. 146).

Osteopygis Cope

Characterization.—Skull with broadly rounded snout, no deep pit behind premaxillary beak. Mandible with fairly flat triturating surface. Carapace oval, moderately arched and consisting of thick plates. Nuchal plate more than half as long as wide. First peripheral not encroaching upon nuchal from the side. Postero-lateral marginals wide. Upper suprapygal much wider than lower one. Costo-peripheral fontanelles absent (rare) or small, but continuous at least laterally. Medial borders of marginal shields lie on peripheral plates. Second peripheral with conspicuous medial pit for reception of anteriormost prong of hyoplastron. Pygal plate long and relatively narrow. Plastron with central

and lateral fontanelles. Hyo-, hypo- and xiphiplastra join sagittally in open suture. Xiphiplastra broad, stout. Epiplastra very small and thin. Axillo-inguinal distance about one-half the width of hyoplastron.

Type of genus.—*O. emarginatus* Cope.

Horizon and locality.—Greensand. New Jersey.

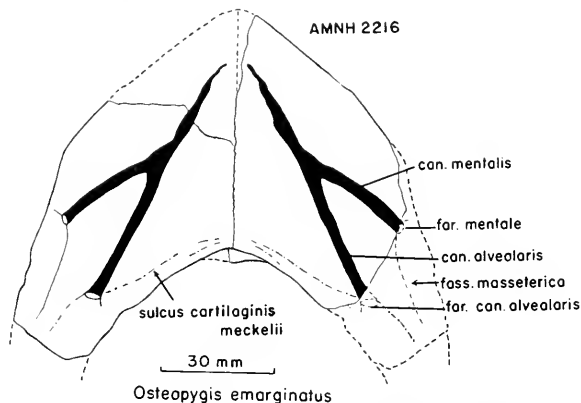


FIG. 85. Internal anatomy of mandible of *Osteopygis emarginatus*. Drawn from X-ray plate.

Discussion.—Up to the time of Hay's revision of the fossil turtles of North America (1908), six species referable to the genus *Osteopygis* had been described, to which list Hay added another and Leidy's doubtful *Chelone sopita*. The latter is based on unsatisfactory type material, consisting of four peripherals. One of these is identified by Hay (1908, fig. 181) as the seventh of the right side. This bone is far too long for its width to belong to the genus *Osteopygis* and has the proportions of some of the cheloniid turtles. There is, furthermore, some doubt as to the association of the four bones. In view of these circumstances, it would seem justifiable to consider *Chelone sopita* a nomen vanum.

Thus, there remain seven species of *Osteopygis*, all of them from the Greensand deposits of New Jersey. With the exception of the shell Y.P.M. 783, described as *O. gibbi* by Wieland (1904a), all specimens are very fragmentary. A survey of nearly all *Osteopygis* materials in the major collections reveals that there are only a few more specimens than described species and these cannot definitely be identified with any of the seven species. The truth of the matter is that no two specimens agree closely with each other if one uses the criteria that have been proposed to distinguish the numerous forms of Hay's revision. These criteria are: presence or absence of lateral fontanelles in the carapace; presence or absence of notches above and below the rib-pits in the peripherals; thickness of the shell; emargination or lack of such in the posterior peripherals; flattened or round rib-pits; proportions.

According to Hay (1908, p. 128), the eight species are supposed to fall into two groups, namely, with and without lateral fontanelles in the carapace. In the first group, lacking fontanelles, he placed *O. emarginatus*, *O. gibbi*, and *O. robustus*; yet the fifth peripheral of the type specimen of *O. emarginatus* (A.M.N.H. 1485) shows no sign of a medial suture and certainly had lateral fontanelles (fig. 87). *O. gibbi* is distinguished from *O. robustus*, among other features, by peripherals notched by the rib-pits in the former and lack of such notches in the latter. Re-examination of the type material of *O. robustus* reveals that peripheral 10 is unnotched but peripheral 9 is notched as in *O. gibbi* (fig. 86).

Nearly all characters used to distinguish these species are related to aquatic specialization and are highly variable not only in this genus but quite generally. The degree of fontanellization, for instance, varies greatly in *Toxochelys moorevillensis* (pl. 23), and some of the shells have notched peripherals, while others do not.

After careful examination of nearly all available material, I have come to the conclusion that there is only one species represented. The observable differences are individual variations, correlated, for the most part, with marine adaptation. Some may be age differences.

***Osteopygis emarginatus* Cope**

Osteopygis emarginatus Cope, Proc. Acad. Nat. Sci. Phila., p. 147, 1868 (nomen nudum); Cook's Geol. N. J., p. 735, 1868 (1869) (nomen nudum); Amer. Nat., 3, p. 89, 1869; Trans. Amer. Phil. Soc., 14, (n.s.), pp. 135-136, 235, pl. 7, fig. 3, 1870 (1871); Rept. U. S. Geol. Surv. Terr., 2, p. 259, 1875; Hay, U. S. Geol. Surv. Bull., 179, p. 441, 1902; Carnegie Inst. Wash. Publ., 75, p. 129, figs. 134-141, 1908.

Osteopygis sopita Cope, Proc. Acad. Nat. Sci. Phila., p. 147, 1868; Rept. U. S. Geol. Surv. Terr., 2, p. 258, 1875; Hay, U. S. Geol. Surv. Bull., 179, p. 441, 1902.

Osteopygis borealis Hay, Carnegie Inst. Wash. Publ., 75, p. 141, pl. 25, fig. 3, text figs. 163-171, 1908.

Osteopygis platylomus Cope, Amer. Nat., 3, p. 89, 1869; Cook's Geol. N. J., p. 735, 1868 (1869); Trans. Amer. Phil. Soc., 14, (n.s.), pp. 135, 137, figs. 38, 39, 1870 (1871); Rept. U. S. Geol. Surv. Terr., 2, p. 258, 1875; Hay, U. S. Geol. Surv. Bull., 179, p. 441, 1902; Carnegie Inst. Wash. Publ., 75, p. 146, figs. 172-180, 1908.

Osteopygis gibbi Wieland, Amer. Jour. Sci., (4), 17, p. 118, pls. 5-8, text figs. 3-7, 1904; Hay, Carnegie Inst. Wash. Publ., 75, p. 132, pl. 26, fig. 1, pl. 27, figs. 1, 2, text figs. 142-146, 1908.

Osteopygis robustus Hay, Carnegie Inst. Wash. Publ., 75, p. 134, figs. 147-151, 1908.

Osteopygis erosus Cope, Rept. U. S. Geol. Surv. Terr., 2, p. 258, 1875; Hay, U. S. Geol. Surv. Bull., 179, p. 441, 1902; Carnegie Inst. Wash. Publ., 75, p. 138, pl. 26, fig. 2, text figs. 155-162, 1908.

Osteopygis chelydrinus Cope, Proc. Acad. Nat. Sci. Phila., p. 147, 1868 (nomen nudum); Cook's Geol. N. J., appendix, p. 735, 1869 (nomen nudum); Amer. Nat., 3, p. 89, 1869; Trans. Amer. Phil. Soc., 14, (n.s.), pp. 135, 138, pl. 7, fig. 8, 1870 (1871); Hay, U. S. Geol. Surv. Bull., 179, p. 441, 1902; Carnegie Inst. Wash. Publ., 75, p. 136, pl. 23, figs. 4-7, pl. 28, figs. 1-4, text figs. 152-154, 1908.

Catapleura chelydrina Cope, Rept. U. S. Geol. Surv. Terr., 2, p. 259, 1875.

Propleura sopita Cope, Cook's Geol. N. J., p. 735, 1868 (1869); Amer. Nat., 3, p. 88, 1869; Trans. Amer. Phil. Soc., 14, (n.s.), pp. 140, 235, pl. 7, figs. 4-7, text fig. 39, 1870 (1871).

Osteopygis emarginatus

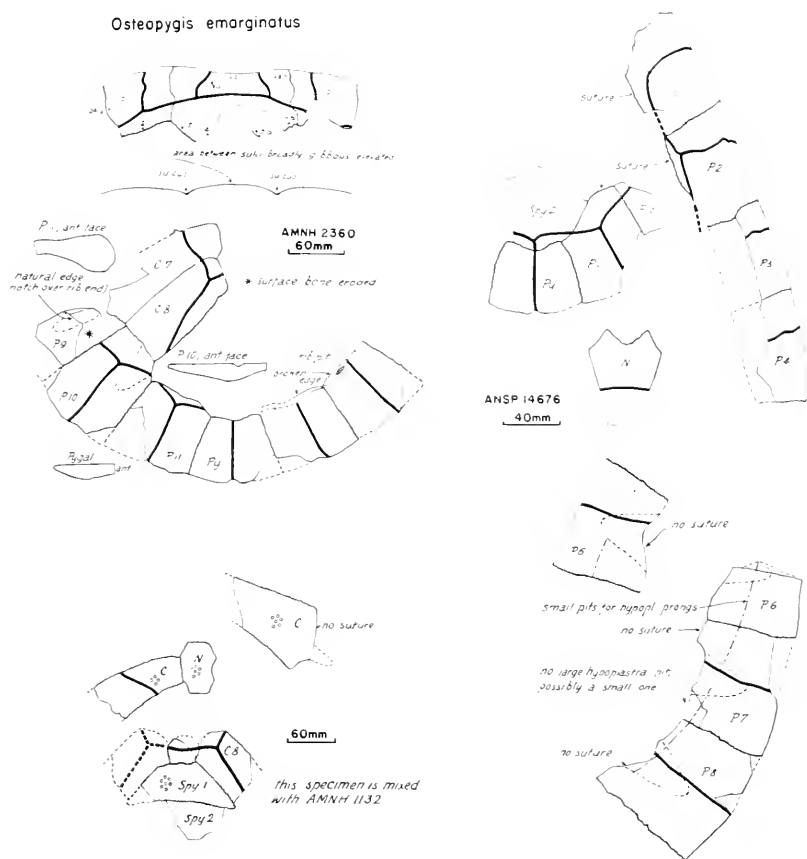
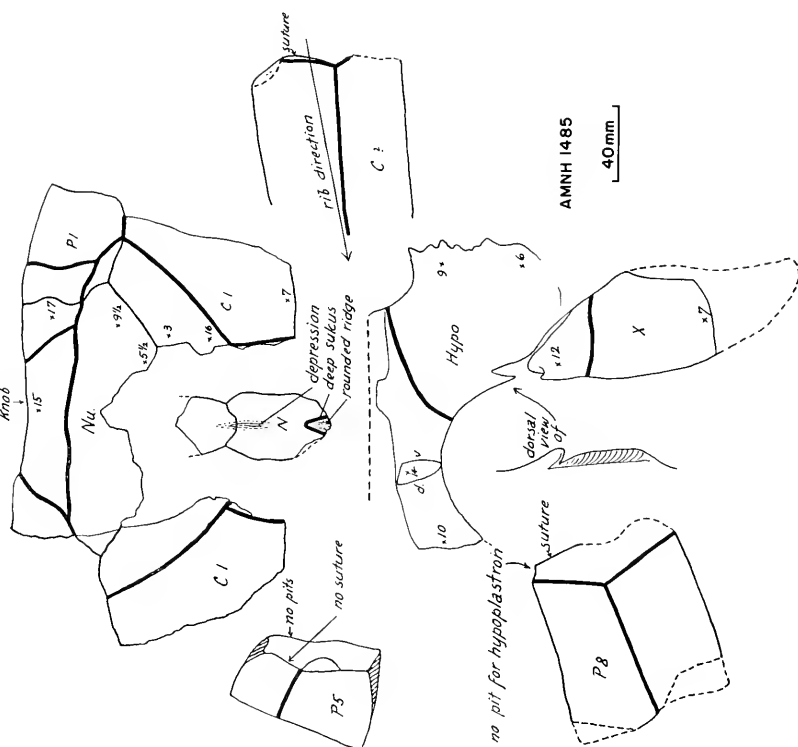


FIG. 86. *Osteopygis emarginatus*. Annotated sketches made from originals.

- Propleura borealis* Wieland, Amer. Jour. Sci., (4), 17, p. 129, pl. 9, 1904; Amer. Jour. Sci., (4), 18, p. 190, fig. 4, 1904.
- Lytoloma angusta* Cope, Trans. Amer. Phil. Soc., 14, (n.s.), p. 145, pl. 11, figs. 1, 1a, 1870 (1871) (part); Hay, Carnegie Inst. Wash. Publ., 75, p. 155, pl. 28, fig. 5, 1908 (part); Wieland, Amer. Jour. Sci., (4), 18, p. 183, figs. 1, 2, 1904.
- Lytoloma wielandi* Hay, Carnegie Inst. Wash. Publ., 75, p. 157, pl. 28, figs. 7, 8, pl. 29, fig. 1, 1908 (in part).
- Erquelinnesia molaria* Hay, Carnegie Inst. Wash. Publ., 75, p. 160, figs. 198, 199, 1908.

no subnuchal
Knob



no subnuchal
Knob

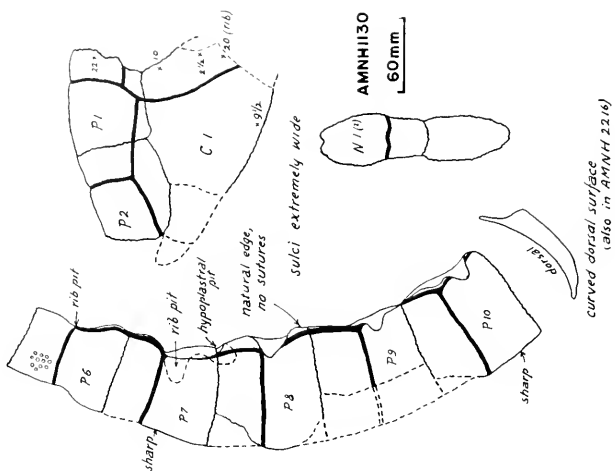


FIG. 87. *Osteopygis emarginatus*. Annotated sketches made from originals.

Osteopygis emarginatus

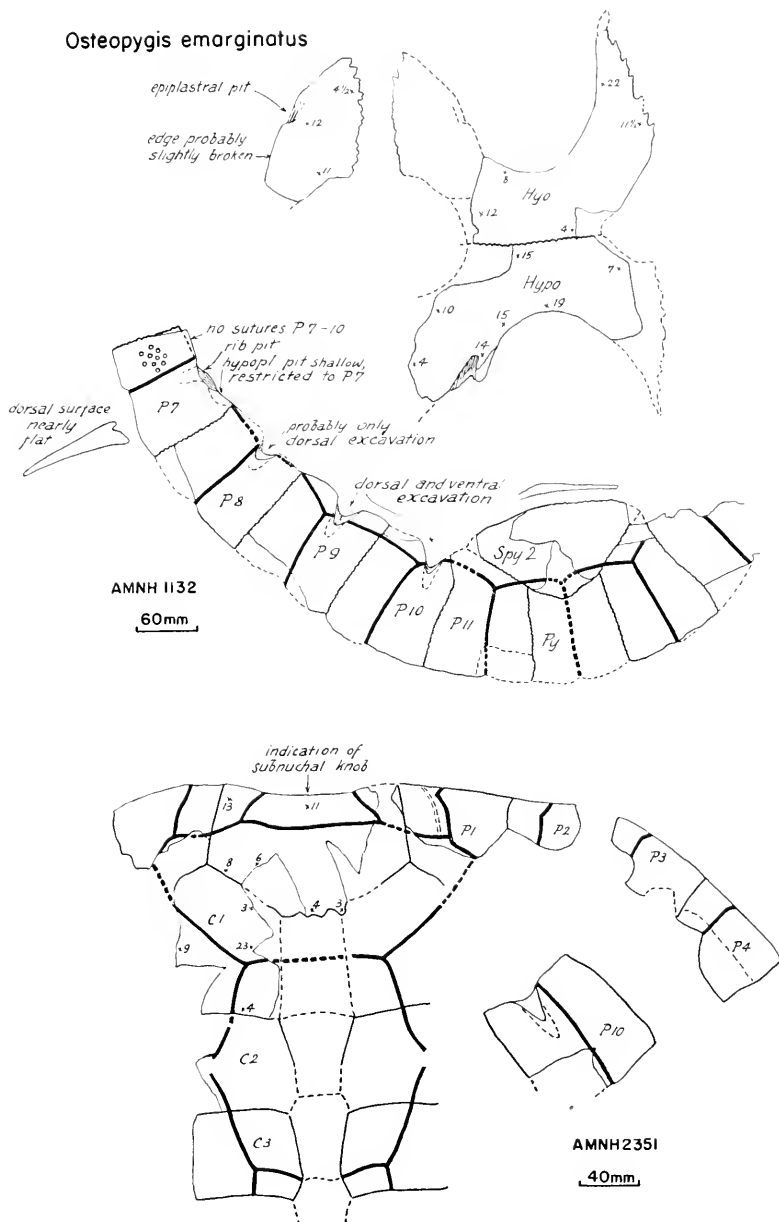


FIG. 88. *Osteopygis emarginatus*. Annotated sketches made from originals.

Type.—A.M.N.H. 1485, type of *Osteopygis emarginatus* (fig. 87).

Horizon and locality.—Greensand. Barnesboro, New Jersey.

Referred specimens.—A.N.S.P. 14676, type of *O. platylomus*, Pemberton, New Jersey (fig. 86); Y.P.M. 778, type of *O. borealis*, Hornerstown, New Jersey (pl. 26); A.M.N.H. 1132, partial rim of carapace, partial plastron, which may not belong to the same individual, Hornerstown, New Jersey (fig. 88); A.M.N.H. 1132, another specimen with the same number (fig. 86); A.M.N.H. 2351, fragmentary anterior portion of carapace, Birmingham, New Jersey (fig. 88); A.M.N.H. 2360, type of *O. robustus*, Birmingham, New Jersey (fig. 86); A.M.N.H. 1130, type of *O. erosus*, Barnesboro, New Jersey (fig. 87); Y.P.M. 783, type of *O. gibbi*, Barnesboro, New Jersey (fig. 89); A.M.N.H. 1131, type of *O. chelydrinus*, Barnesboro, New Jersey; A.M.N.H. 2216, jaw (pl. 16, fig. 1, b) and parts of shell, New Jersey; Y.P.M. 1001, jaw, Hornerstown, New Jersey (pl. 16, fig. 1, d); Y.P.M. 490, jaw, Hornerstown, New Jersey (pl. 16, fig. 1, c); Y.P.M. 602, jaw, Birmingham, New Jersey; Y.P.M. 3613, several jaw fragments, Hornerstown, New Jersey; Y.P.M. 913, jaw, Hornerstown, New Jersey (pl. 16, fig. 1, a); Y.P.M. 913a, anterior region of skull, Hornerstown, New Jersey (fig. 61); Y.P.M. 734, fragmentary specimen, New Jersey; Y.P.M. 991, fragmentary specimen, New Jersey; A.M.N.H. 2870, seven peripherals, New Jersey; Y.P.M. 1585, nuchal, anterior peripheral and fragments, Mullica Hill, New Jersey; A.N.S.P. 9220, jaw, type of *Erquelinnesia molaria*, Birmingham, New Jersey; A.M.N.H. 1133, fragment of jaw, Birmingham, New Jersey.

The present procedure of including all materials listed above in one species resulted from the realization that the fragmentary specimens do not permit the recognition of more than one form. But the possibility of the existence of more than one species in all of the Greensand deposits is undeniable. Additional material, more carefully collected than in the past, is required to decide this matter.

Amended diagnosis.—As for the genus.

Discussion.—Y.P.M. 913a presents the snout region of the only known skull referable to *Osteopygis* (fig. 61). It has been described and illustrated by Wieland (1904a, fig. 2) and by Hay (1908, pl. 28, figs. 7, 8, pl. 29, fig. 1). The palatal face of this fragment is remarkable because of the unusual relative flatness of the triturating surface, outwardly bordered by a very low alveolar ridge. As in the Recent *Caretta* and in contrast to *Chelonia*, the triturating surface does not form sharp, masticatory ridges; instead, it has a low, broadly rounded elevation that runs in a blunt arc from one side of the triturating surface to the other, approximately parallel to the alveolar border, thus differing in detail also from *Caretta*. Posteriorly, the triturating shelves of the maxillae are greatly expanded, almost excluding the palatine bones from the formation of the secondary palate. The ventral plate of the vomer is wider than the combined width of the premaxillae and forms a broad sutural contact with them. The vomerine pillar, separating the narial passages, is stout and extends to the posterior end of the ventral plate (thus to the rim of the choanal opening), differing markedly from *Caretta*, where the pillar ends a notable distance farther forward. The dorsal,

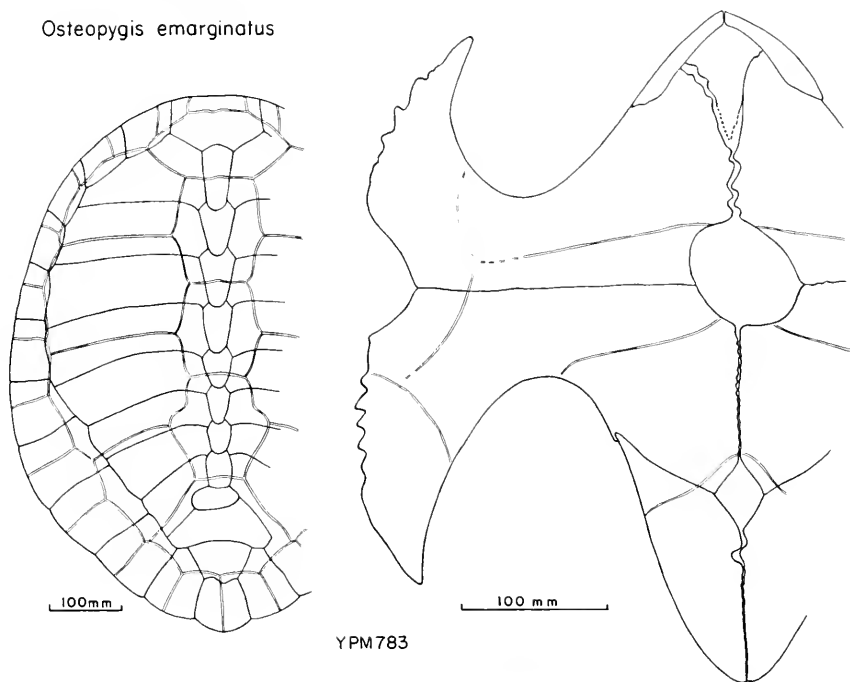
Osteopygis emarginatus

FIG. 89. Carapace and plastron of *Osteopygis emarginatus* (Y.P.M. 783). After Wieland.

expanded portion of the vomer shows a pronounced sagittal sulcus that runs backward to the broken edge of the bone. A similar longitudinal groove is absent in *Caretta caretta*. Furthermore, the descending processes of the prefrontals join the dorsal plate of the vomer in a posteriorly extended, horizontal suture. In *C. caretta*, this suture area is smaller and does not reach as far backward.

On the whole, this skull fragment of *Osteopygis* resembles the corresponding area of the skull of *Caretta*, but, in detail, there are numerous differences throughout, which should be expected if my interpretation of a convergence with the cheloniid turtles is correct.

In so far as the surface bone is well preserved, the mandibles (pl. 16) are of fairly uniform appearance. In most specimens, the triturating surface is divided along the symphysis into two slightly concave areas by an obtuse elevation. The latter is more pronounced in front, where it forms a blunt ridge. Posteriorly, it is merely a gradual increase in thickness of the triturating shelf toward the symphysis. In A.M.N.H. 2216 and in A.N.S.P. 9220, the triturating surfaces are nearly flat. Compared to *Toxochelys*, the medial face of the masticatory portion of the mandibular ramus is greatly shortened but it is provided with a deep sulcus (fig. 85, sulcus cartilaginis meckelii) and a sagittal pit that

extends forward along the symphysis. Presumably, the meckelian cartilages entered into this pit for an undetermined distance. Directly below the most posterior point of the triturating surface in each ramus the canalis alveolaris opens into the meckelian sulcus (fig. 85). On the lateral side of the ramus, at the foremost point of the masseteric fossa, there is a large foramen mentale. X-ray plates of all these jaws reveal that the canalis alveolaris and the canalis mentalis meet below the center of the triturating surface in each ramus (fig. 85), and a single canal of decreasing caliber runs forward to a point some distance behind the tip of the jaw. The angle formed by the alveolar canals varies from 50° to 62° and the observed range of the length-width index of the triturating surface is 70.5 to 79 (see p. 205) among the seven specimens at hand. On the ventral face of some of the jaws, the posterior extent of the horny beak is marked by a shallow impression. It begins laterally directly in front of the foramen mentale, arches slightly forward and then backward and reaches the posterior end of the symphysis.

Only one complete shell of *Osteopygis* is known (Y.P.M. 783), the remaining specimens being rather fragmentary (see figs. 86–89). Since seven species have been based on these materials, it was felt that new illustrations—based on my own drawings of the specimens along with pertinent comments—should be rendered for future consideration of the species question.

The carapace of *Osteopygis* is oval and rather highly arched. The thickness of the shell plates differs, of course, in different areas of the shell, as usual, but, on the whole, the plates are thick (see comments on drawings). The degree of fontanellization varies from none (Y.P.M. 783) to fontanelles laterally in the vicinity of peripheral 5 but not extending backward beyond peripheral 7 (A.M.N.H. 1485), to continuous fontanellization from opposite the third to opposite the tenth peripheral. This is not actually observable in any one specimen, but A.M.N.H. 2870, A.M.N.H. 1130, and Y.P.M. 778 make the supposition probable. Peripherals 1, 2, and 11 are suturally connected with the costal disk in all specimens. The situation observed in *Porthochelys* and *Thinochelys* is not found among these specimens, but it should probably be expected to occur. The peripherals of *Osteopygis* indicate clearly that the plastron was in relatively intimate contact with the carapace. There is a deep pit on the visceral side of the second peripheral, which received the large antero-lateral prong of the hyoplastron (pl. 26). A similar pit for the reception of the postero-lateral prong of the hypoplastron is located on the visceral side of the seventh peripheral (A.M.N.H. 1132), or it may be so deep as to lie across the suture between the seventh and eighth peripherals (A.M.N.H. 1130). Small pits along the ventro-medial edges of some of the lateral peripherals, corresponding to the smaller hyo- and hypoplastral prongs, are not seen in all specimens, reflecting differences in the degree of ossification of the plastra. The medial furrows of the marginal scutes lie on the peripherals, though very close to their inner edges. In specimens with notable fontanelles, they overlie the vacuities. In the postero-lateral peripherals, the ribs may enter regular pits dorsally and ventrally covered by

thin sheets of bone. In some cases, however, these pits may be more or less exposed above or below or both (A.M.N.H. 1132). This feature is subject to variation. Similar conditions are seen less frequently in *Toxochelys moorevillensis*. The upper suprapygals are much larger than the lower suprapygals, the reverse from what it is in *Thinochelys*. The pygal is longer than wide anteriorly.

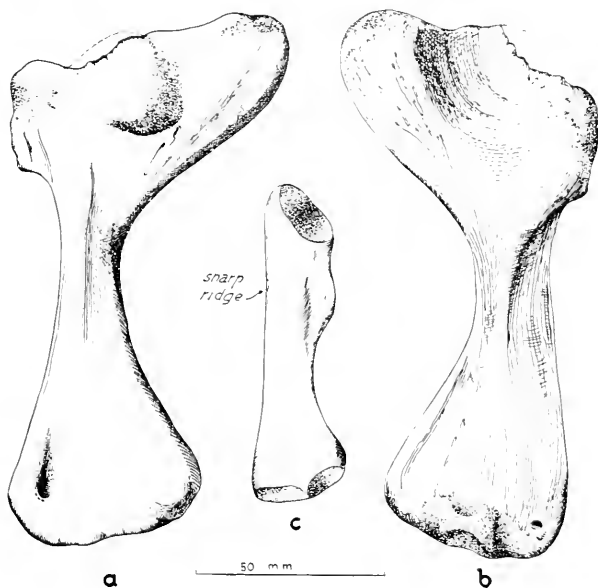


FIG. 90. Humerus and left ulna of *Osteopygis emarginatus* (Y.P.M. 783).

The plastron is characterized by wide lateral expansion of hyo- and hypoplastra. The suture between these plates is very long. The umbilical fontanelle is more or less circular and there are notable lateral fontanelles. The pattern of the plastral shields is indicated in figure 89; it is essentially like that of *Toxochelys* (see *T. weeksi*, fig. 78). It is virtually certain that there was a series of inframarginal scales, but these shields rarely leave imprints on plastra that are partially reduced laterally (for example, in Recent Chelydridae, Dermatemyidae, and Cheloniidae). The shield pattern at the anterior end of the plastron is unknown. The limited girdle and limb material is discussed on page 206.

Incertae sedis

Rhetchelys platyops (Cope)

Euclastes platyops Cope, Proc. Acad. Nat. Sci. Phila., p. 41, 1867; Cook's Geol. N. J., p. 735, 1868 (1869); Amer. Nat., 3, p. 89, 1869; Trans. Amer. Phil. Soc., 14,

(n.s.), p. 149, pls. 6, 7, fig. 9, 1870 (1871); Rept. U. S. Geol. Surv. Terr., **2**, p. 259, 1875.

Lytoloma platyops Hay, U. S. Geol. Surv. Bull., **179**, p. 442, 1902; Wieland, Amer. Jour. Sci., (4), **18**, p. 185, 1904.

Rhetechelys platyops Hay, Carnegie Inst. Wash. Publ., **75**, p. 162, pl. 29, figs. 2, 3, 1908.

Type.—A.N.S.P. 10187, a large, partially damaged skull.

Horizon and locality.—Late Cretaceous. Hurffsville, Camden County, New Jersey.

Discussion.—Hay (1902) proposed the generic name *Rhetechelys* for this form and placed it near *Erquelinnesia*. Although I have seen the specimen, side by side comparison with the snout fragment of *Osteopygis* (Y.P.M. 913a) was not possible. In so far as the published illustrations permit comparison, the differences between the specimens are as follows: There is a deep pit behind the premaxillary beak in *Rhetechelys* that suggests a sharp upturned point on the mandible, a feature not present in *Osteopygis* and not observed in typical development in any toxochelyid turtle. The snout area of *Rhetechelys*, furthermore, is distinctly more slender and more pointed than in *Osteopygis*. *Rhetechelys* is a very large form. None of the mandibles of *Osteopygis* are large enough to fit this animal. The length of the symphysis in *Caretta caretta* amounts to about 80 per cent of the sagittal extent of the secondary palate. The symphysis of the largest mandible of *Osteopygis* (A.N.S.P. 9220) measures only 68 per cent of the palatal length of *Rhetechelys*. The greater part of the braincase and the squamosal region are missing, so that it is, at present, impossible to allocate *Rhetechelys* to, or reject it from, the Osteopyginae with reasonable confidence.

Subfamily **Lophochelyinae** nov.

Characterization.—Specialized toxochelyid turtles. Skull with a technically primary palate, but somewhat specialized in the direction of an undershelfing of the internal nasal openings. Triturating surfaces wider than in the Toxochelyinae. Anterior vomer area narrow and rough. Small nasal bones. Upper and lower shelves of mandible at symphysis of nearly equal width. Shell consisting of thin plates. Carapace oval to cordiform in outline. Neuralia serrated, forming mid-dorsal keel. Epineural elements in *Ctenochelys* and *Prionochelys*. Peripheral edge of carapace moderately to strongly serrated. Costo-peripheral fontanelles always large, extending forward at least to the second peripheral plate. Connection between pygal and suprapygal very narrow or entirely broken. A pair of post-nuchal fontanelles, at least in young forms. Plastron with large central and lateral fontanelles. Hyo-, hypo- and xiphiplastra with conspicuous ventral keel knobs.

Lophochelys, Ctenochelys, Prionochelys

Discussion.—Useful skull material is known in the genera *Ctenochelys* and *Prionochelys*. An adequate characterization of the morphology of the skull

within the subfamily is, however, not yet possible. The skull is more robust than that of *Toxochelys* and readily distinguished from the latter by the wide triturating surfaces that encroach significantly upon the lateral edges of the palatines and the vomer. Thus, the development of a secondary palate is here initiated. The basisphenoid (fig. 100) is much as in *Chelonia* (pl. 9), but the course of the carotid canal is more nearly like that of *Chelydra*.

The carapace is characteristically possessed of a serrated mid-dorsal keel and a serrated marginal edge. These two features are strictly correlated with each other and with the partial undershelfing of the palate in the family Toxochelyidae. No form is known that has only one or two of these characters. The dorsal keel may be formed simply by crested, thecal neural plates (as in *Lophochelys*), or it may contain epithecal ossicles that produce conspicuous keel elevations beneath the apices of the vertebral shields (as in *Ctenochelys*), or, finally, modified thecal neural plates, in conjunction with large epithecal elements, may form large keel elevations (as in *Prionochelys*). Lateral fontanelles are always present and large, even in adult individuals. Furthermore, there are post-nuchal fontanelles, except in large individuals of *Prionochelys nauta*, where such fontanelles are absent (but probably will be found in smaller specimens) and where the lateral fontanelles are relatively small, though continuous.

The plastron is not as characteristic as the carapace. Compared to the Toxochelyinae, it exhibits larger central and lateral fontanelles in the adult.

Because of the unsatisfactory state of preservation of most of the material, it is not yet possible to work out the basic morphology of the girdle and limb skeleton within the subfamily.

Lophochelys gen. nov.

Characterization.—Most primitive genus of subfamily. Skull unknown. Neural carina lacking epithecal plates, except possibly in most posterior part of carapace. Peripheral serration of carapace moderate. No connection between pygal and suprapygal in young; adult condition unknown. A pair of post-nuchal fontanelles.

Type of genus.—*Lophochelys natatrix*.

Horizon and locality.—Niobrara Formation, Late Cretaceous. Kansas.

Discussion.—The genus *Lophochelys* is represented by three species, *L. natatrix* and *L. niobrarae* from the Niobrara Chalk of Kansas, and *L. venatrix* from the Mooreville Chalk of Alabama. The skull is not known at present. The carapace has a mid-dorsal carina, serrated in side view, with the apices corresponding to the apices of the vertebral shields. No epithecal ossicles are involved in the construction of the carina, except possibly in the posterior area of the shell. The evidence is subject to some doubt, and the observed "suture scars" might be mere erosion surfaces. The marginal edge of the carapace is scalloped, as in *Ctenochelys stenopora* and *C. tenuitesta*. There was apparently no bony connection between the pygal and the upper suprapygal plates. The anterior face of the pygal and the posterior end of the suprapygal show indications that the

connection was by an especially tough strand of connective tissue in the juvenile; the adult condition is unknown. This region of the shell is different, however, from that in *Ctenochelys*, as a comparison of juvenile individuals of both genera reveals (figs. 92, 108). In *Ctenochelys*, a bony lower suprapygial is indicated by an anterior suture projection on the pygal.

The plastron resembles rather closely that of *Ctenochelys*.

The Niobrara species are based on juvenile specimens, which makes comparison with the subadult and adult materials from the Mooreville Chalk very difficult. The most obvious features that appear to separate them are differences in the degree of ossification of the shell, and these are definitely correlated with size and age.

Lophochelys natatrix sp. nov.

Type.—C.N.H.M. PR220, partial carapace and plastron, scapulae, coracoid, limb-bones, vertebrae. Juvenile. Collected by Mr. G. F. Sternberg.

Horizon and locality.—Niobrara Formation, Late Cretaceous. One mile north of the Pyramids, Logan County, Kansas.

Referred specimen.—Y.P.M. 3606, peripherals, neurals. Locality?, Niobrara Formation, Late Cretaceous.

Diagnosis.—Carapace oval, pointed posteriorly. Nuchal plate less than three times as wide as long; slightly excavated in front. No preneural. First pair of costal plates embraces only anterior half of first neural. Neural plates hexagonal, with antero-lateral and postero-lateral sides approximately equal in length. Pygal plate at mid-line half as long as wide. Peripherals of normal width. Plastron with pronounced keel bosses.

Description.—Both specimens referred to this species are juveniles. The type specimen contains enough skeletal material to permit an accurate characterization of the shell (figs. 91, 92). The carapace is oblong, moderately pointed behind, gently arched and greatly fontanelized. The latter is certainly a feature of age. The edge of the carapace is moderately serrated, much as in *Ctenochelys tenuitesta* and *C. stenopora*. The relatively long and narrow peripheral bones are those of immature individuals, and proportionately wider elements are to be expected in adults. The nuchal plate is slightly excavated in front and notably arched from side to side. The neural series consists of hexagonal plates whose antero-lateral and postero-lateral sides are of nearly equal length. The first neural is sharply crested and forms a keel apex anterior to the transversal shield furrow (fig. 91). A small, posterior neural, still suturally united to fragments of the adjoining elements, has a longitudinal scar along its ridge line. It may have borne an epithecal ossicle, or the scar may be an erosion surface. The matter cannot be decided. The first pair of costal plates embraces only the anterior half of the elongated first neural, namely, back to the level of its greatest width. The costo-nuchal sutures slant forward and outward. The nuchal shield is very short; its posterior furrow lies very close to the cervical margin of the nuchal plate (figs. 91, 92).

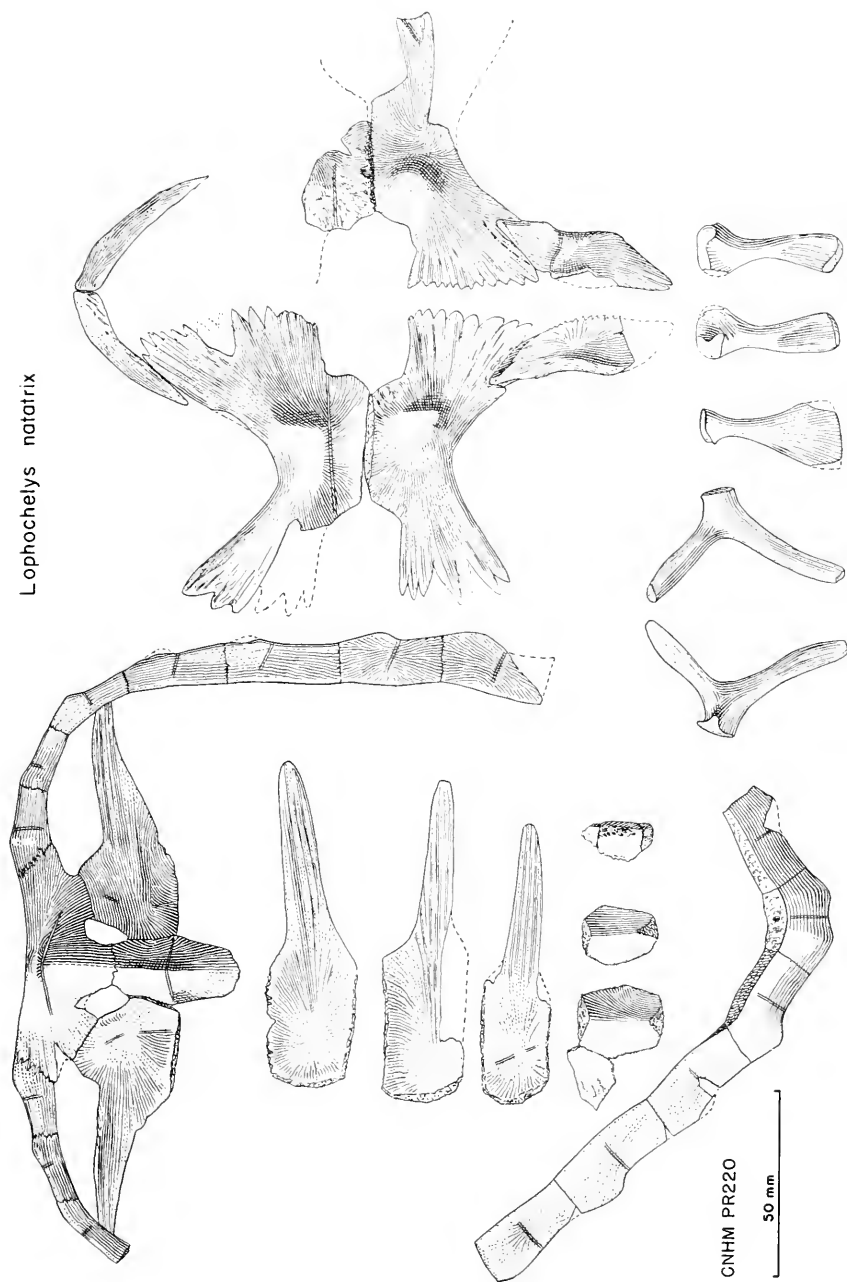


FIG. 91. *Lophochelys natatrix* (C.N.H.M. PR220). Carapace, plastron, girdle, and limb-bones of type specimen.

In the type specimen and in Y.P.M. 3606, the pygal is of normal shape. The anterior face is entirely smooth. If PR220 and Y.P.M. 3606 are compared with the likewise juvenile type specimen of *C. stenopora*, K.U. (V.P.) 1205—about the same size as PR220—the pygal plate of the latter is seen to possess a marked sagittal projection facing the suprapygal region (fig. 108). The lack of a similar process in *L. natatrix* suggests that the pygal-suprapygal connection was effected by connective tissue only.

The beautiful plastron of PR220 is clearly that of a young individual with larger fontanelles than should be expected in an adult. Hyo-, hypo- and xiphiplastra have pronounced ventral keel bosses. An isolated plastron of this species should be difficult to distinguish from that of *C. stenopora*; the xiphiplastra with their acute postero-lateral angles differ, however, considerably from those of all known specimens of *C. stenopora*.

The eighth cervical vertebra has a short centrum and a deep, single concavity in front. The neurapophysis has a well-developed dorsal platform that indicates the original presence of a ventral knob on the nuchal, which shows merely a lesion in the surface bone where the knob has been.

The scapula, coracoid and femur are shown in figure 91. The distal expansion of the coracoid is exaggerated by crushing.

Lophochelys niobrarae sp. nov.

Type.—C.N.H.M. UR1, partial carapace. Juvenile.

Horizon and locality.—Niobrara Formation, Late Cretaceous. Kansas.

Referred specimens.—C.N.H.M. UR2, plastron of an individual the size of UR1; horizon and locality as for UR1. C.N.H.M. UR7, partial plastron, pygal plate, ilium; horizon and locality as for UR1.

Diagnosis.—Carapace oval, not pointed posteriorly. Nuchal plate about three times as wide as long; slightly excavated in front. No preneural. First pair of costals embrace first neural entirely. First neural without keel ridge or keel apex anterior to transverse shield furrow. Anterior neural plates much longer than wide, hexagonal with very short antero-lateral and long postero-lateral sides. Pygal plate at mid-line only one-fifth its width. Peripherals probably very narrow. Plastron with indistinct keel bosses.

Description.—It is, indeed, unfortunate that there is no way of determining satisfactorily whether UR2 is the plastron of UR1. The type of preservation, lack of crushing and perfect surface texture, light beige color of the bones and the size strongly suggest it. The available records indicate that both specimens were collected by Harold T. Martin and purchased in 1894, together with a small number of other fragmentary turtle remains, among them UR7. The latter is differently preserved and severely flattened; the surface texture is poor, the color is dark brown and the specimen is more than twice the size of UR1 and UR2.

The differences in size and preservation of UR2 and UR7 render comparison between corresponding parts all but impossible. Additional collections will be

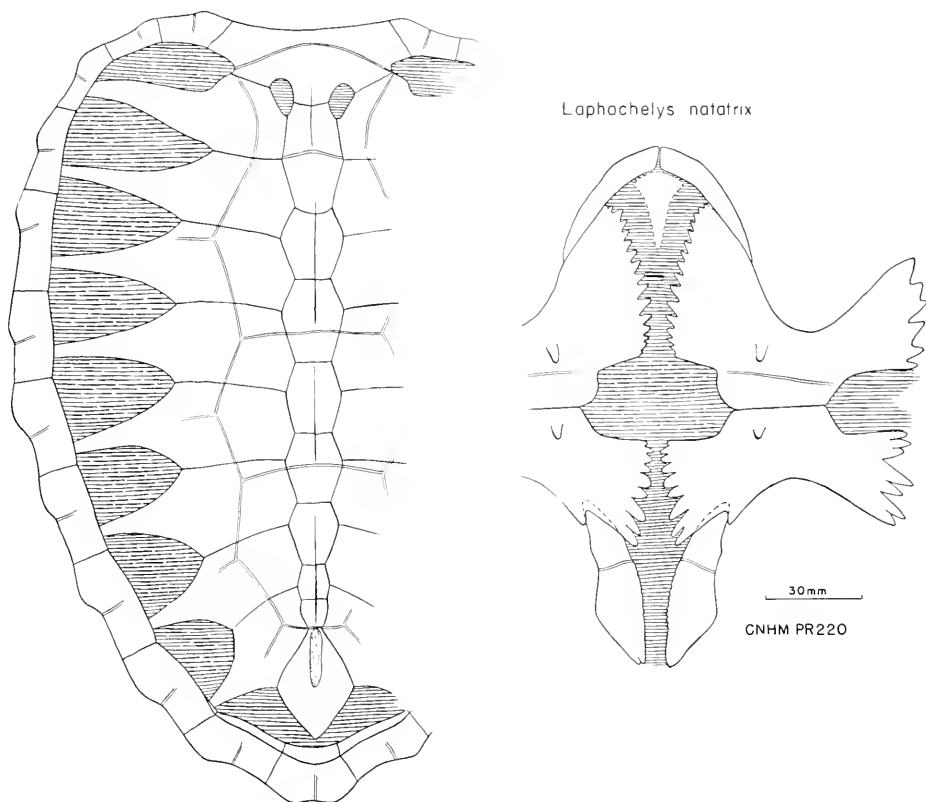


FIG. 92. *Lophochelys natatrix* (C.N.H.M. PR220). Reconstruction of carapace and plastron.

required to determine whether the reference of UR2 to this species is correct. If so, it probably belongs to the type carapace, UR1.

The type, UR1, is an unusually well-preserved carapace of a very juvenile individual of about 175 mm. carapacial length. It lacks all of the peripherals, but the short and wide pygal plate (fig. 94) is present. The shape of this bone is that expected of an early ontogenetic stage of ossification, growing, with age, to the shape of any typically toxochelyid pygal. This interpretation would undoubtedly be in order were it not for the fact that the pygal of UR7, a much larger individual, shows no change in proportion in the expected direction. It is very short and wide, as in UR1. The pygal of C.N.H.M. PR220 (type of *L. natatrix*), which is about half the size of UR7, has a normally proportioned pygal (fig. 91); the same is true of Y.P.M. 3606 (fig. 93), an even smaller individual than PR220. In view of this, it must be assumed that the pygal plate

(and of necessity the peripherals) of *L. niobrarae* show a retardation or even arrestation of growth at an early stage of ossification. The neural plates of UR1 are well documented either by the bones themselves (nos. 1, 3, 4, 5, 6, 9) or by their outline, formed by the adjoining costal plates (nos. 2, 7, 8). In contrast to *L. natatrix*, the dorsal keel ridge begins behind the first neural, which is an

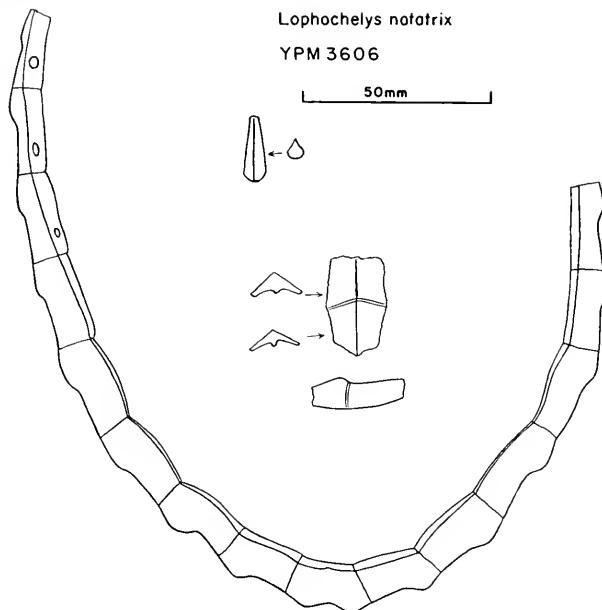


FIG. 93. Peripherals and neural of *Lophochelys natatrix* (Y.P.M. 3606).

almost flat plate. The lateral corners of all the neurals are sharply defined, which is not the case in *L. natatrix*. The antero-lateral sides of the hexagonal neurals are very short in neurals 2 to 5, shorter than the postero-lateral sides in neurals 6 and 7, and the two are of equal length in neural 8. The ninth of the series is elongated and deeply inserted into the anterior margin of the suprapygal (fig. 94). The nuchal is relatively shorter and wider than in *L. natatrix* (fig. 94).

The beautifully preserved plastron, UR2, is characterized by thick hyo-, hypo-, and xiphiplastrs, with keel bosses that are not particularly conspicuous—far less so than in *L. natatrix* (PR220). The xiphiplastrs are relatively stout and rather wide and blunt posteriorly. The plastral fragments of UR7 are so crushed that their original thickness cannot be determined. They agree with UR2 in having only indications of keel bosses. The shape of the posterior end of the xiphiplastron of UR7 differs notably from that of UR2; it resembles PR220, *L. natatrix*.

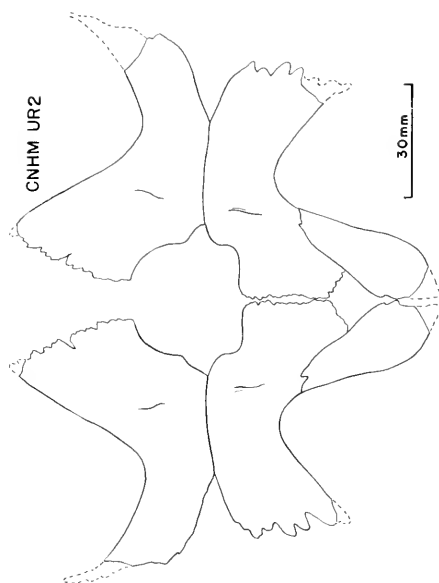
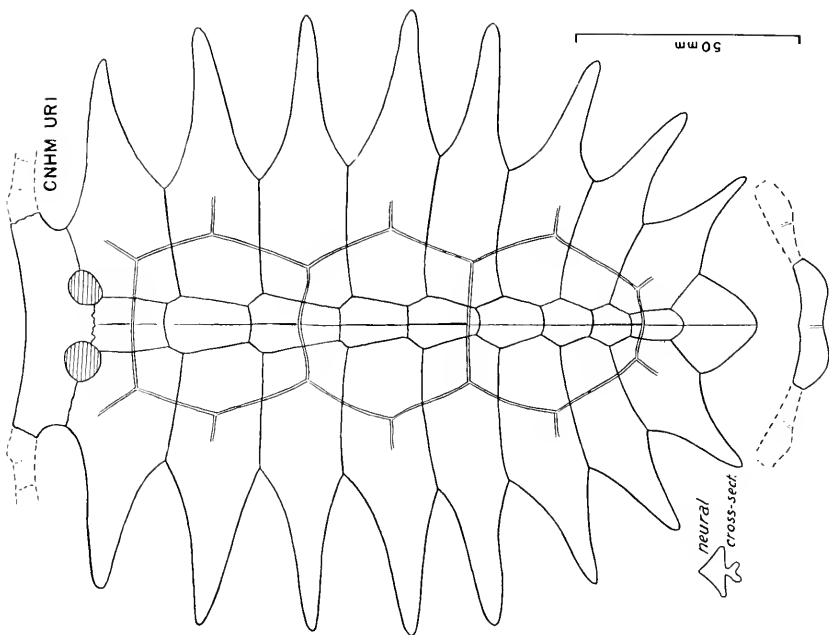


FIG. 94. Carapace (C.N.H.M. UR1) and plastron (C.N.H.M. UR2) of *Lophochelys niobrarae*.

Lophochelys venatrix sp. nov.

Type.—C.N.H.M. P27355, fragmentary specimen.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Moore Brothers farm, Harrell Station area, Dallas County, Alabama.

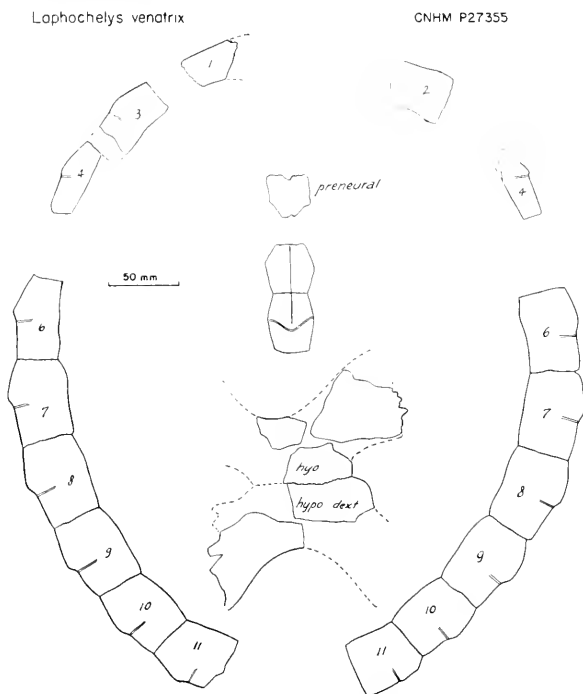
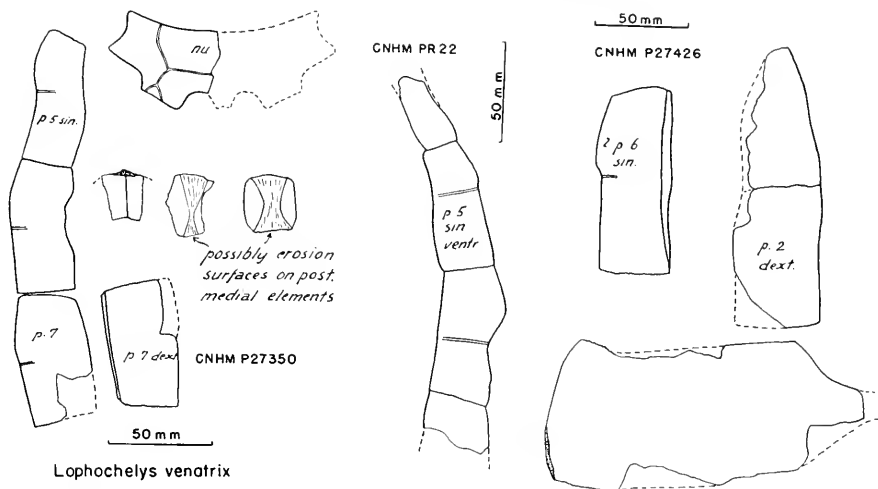


FIG. 95. Type specimen of *Lophochelys venatrix* (C.N.H.M. P27355).

Referred specimens.—Harrell Station area, Dallas County, Alabama: C.N.H.M. P27426, peripherals and costal plates; C.N.H.M. P27350, nuchal, peripherals. Mt. Hebron area, Greene County, Alabama: C.N.H.M. PR22, three peripherals.

Diagnosis.—Carapace broadly oval, rounded posteriorly. Nuchal plate one-third as long as wide, strongly excavated in front. A preneural. First pair of costal plates embrace preneural and anterior half of first neural. First costal forms sutural connection with second peripheral. Possibly an epithecal ossicle in suprapygal region. Lateral fontanelles much narrower than lateral extent of adjoining costals. Nuchal scale large; its posterior furrow at about mid-length of nuchal plate.

Among the keeled turtles of the family Toxochelyidae, from the Mooreville Chalk of Alabama, there is a form, poorly known at present, that does not possess

FIG. 96. Specimens of *Lophochelys venatrix*.

epineural elements. As in *L. natatrix*, there is possible evidence in this form that an epithecal element might have been located in the posterior region of the carapace; but here, as there, the evidence is not conclusive, since the "suture scars" on the keel elements might also be erosions of the surface bone.

The type specimen is of medium size and the bones are crushed, though not entirely flattened. It appears certain that the peripherals are much wider now than in life (figs. 95, 97). In side by side comparison of the peripherals with corresponding plates of *Ctenochelys tenuitesta*, there is very little difference in shape, but those of *Lophochelys venatrix* seem to consist of denser bone.

In the type specimen, there is a preneural, an element not observed in *Ctenochelys tenuitesta* but present in *C. acris*, whose peripherals are characteristically different from both *C. tenuitesta* and *L. venatrix*. The nuchal plate is represented by a fragment of the left half in P27350. It differs from that of *C. tenuitesta* by forming a notable segment of the first fontanelle (fig. 97), and from *C. acris* by being much less excavated in front. The inner margin of the first peripheral shows no suture. The second peripheral is peculiar because its inner margin appears to have been suturally joined by the first costal (fig. 95). The evidence is fairly good. The second peripheral is crushed more than the first or the third. It is thus wider than the adjoining plates. Yet its inner margin, only slightly eroded, is so thick that it probably did not face a fontanelle. This feature is shown in the reconstruction (fig. 97). The carapacial disk, formed by the costal and neural plates, was very probably wider than in *Ctenochelys*.

Only fragments are known of the plastron; these are shown in their relative position in figure 95.

The first vertebral shield did not extend as far forward on the nuchal plate as in *Lophochelys natatrix*. Its anterior imprint lies approximately at mid-length of the nuchal (fig. 96). The nuchal shield was thus large.

Lophochelys venatrix

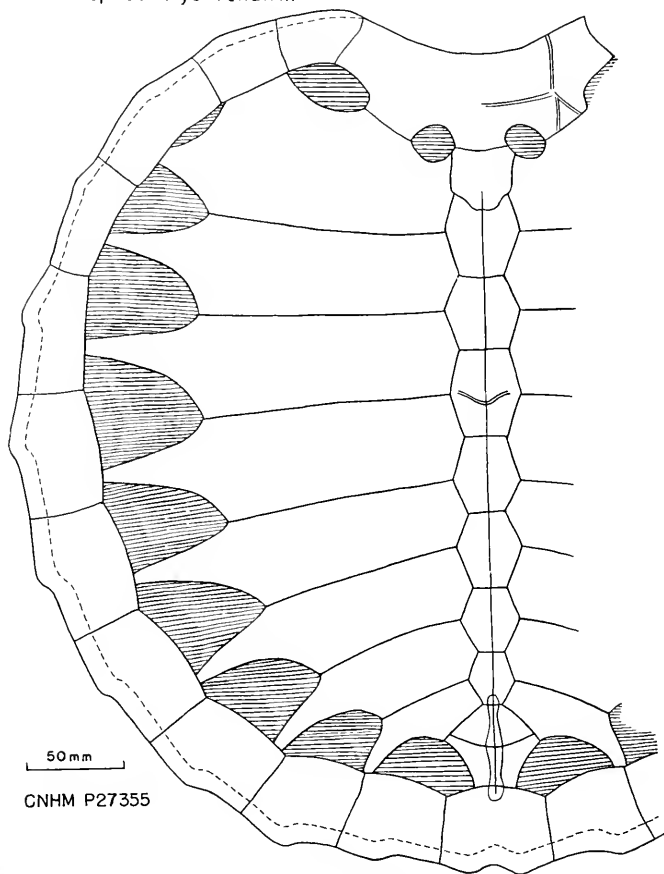


FIG. 97. Reconstruction of *Lophochelys venatrix* (C.N.H.M. P27355). Dotted line indicates probable original width of peripherals. The presence of an epithecal ossicle in the suprapygal area is not certain.

Comparison of *L. venatrix* with *L. natatrix* and *L. niobrarae* is difficult because of the size difference in the specimens. The degree of lateral fontanellization is an age character as well as a feature of aquatic specialization. The degree of shell reduction correlated with the aquatic environment can only be determined on fully mature individuals.

Ctenochelys gen. nov.

Characterization.—Most common genus of subfamily. Skull fairly massive. Anterior portion of vomer narrow and rugose. Triturating surfaces involving significant portions of palatine bones. Mandible massive; triturating shelf widest at symphysis, gradually narrowing toward posterior end. Chin-shelf not protruding posteriorly beyond masticatory shelf. Shell consisting of very thin, spongy plates. Neural carina with epineural elements located below apices of vertebral shields, dorsal to junction of neurals 2 and 3, 4 and 5, 6 and 7; some-

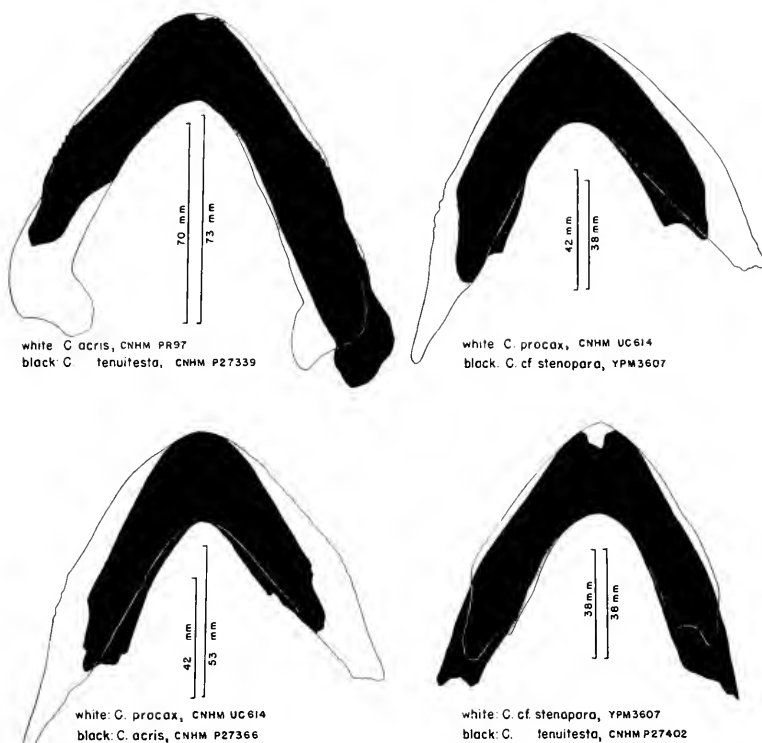
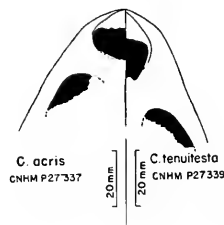


FIG. 98. Comparison of proportions of lower jaw in four species of *Ctenochelys*.

FIG. 99. Proportional differences in snout region of skull in *Ctenochelys acris* and *C. tenuitesta*.



times at junction of pygal and suprapygal. Peripheral edge of carapace moderately to deeply serrated posteriorly; connection between pygal and suprapygal very narrow in adult (condition in young unknown). A pair of post-nuchal fontanelles.

Type of genus.—*Ctenochelys tenuitesta*.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Alabama.

Discussion.—*Ctenochelys* is known both from the Mooreville Chalk of Alabama and from the Niobrara Chalk of Kansas. It is the only genus of the family in which two species can be recognized from both Mooreville Chalk (*C. tenuitesta*, *C. acris*) and Niobrara Chalk (*C. stenopora*, *C. procar*).

C. tenuitesta resembles *C. stenopora* more closely than either *C. acris* or *C. procar*, and the latter two forms appear to be more closely related.

The Mooreville Chalk specimens of *Ctenochelys*, although far from perfect in preservation, are represented in fairly large series. The species identification of fragmentary specimens (depending largely on which parts are preserved) may present difficulties or may be impossible. Specimens of which a fair portion of the skeleton is preserved are readily identified.

The Niobrara Chalk material, on the other hand, poses practically insurmountable difficulties. The number of available specimens is still very limited. Many specimens consist of isolated skulls and/or mandibles, or isolated shell remains. Different age stages are represented and comparisons between them are almost always inconclusive. Finally, the state of preservation ranges from lack of distortion to severe crushing and flattening of the bones. Under these circumstances, needless to say, the revision and species allocation of the materials were complicated and largely indirect procedures, and future discoveries will be required to determine the merit of the present conclusions.

Skull.—Of the ten specimens of cranio-mandibular remains from the Mooreville Chalk, eight were found isolated. The remaining two, both mandibles, are associated with identifiable shell plates of each of the two species. The identification of the eight isolated finds presented thus relatively little difficulty, and the differences between the skulls and mandibles of *C. tenuitesta* and *C. acris* can be characterized as follows: In *C. acris*, both nostril and orbit are relatively much closer to the tip of the snout than in *C. tenuitesta* (fig. 99). The mandibles of the latter species are more slender in the areas of the triturating surfaces than in *C. acris* (fig. 98). This difference is slight, however, and not reliable except in uncrushed specimens.

Only six specimens of *Ctenochelys* consisting of or including cranio-mandibular elements are known to me from the Niobrara deposits. A seventh, an isolated mandible, K.U. (V.P.) 2050, figured by Hay (1908, p. 176) as *C. procar*, is too severely injured to permit identification. Of the six specimens, two are isolated skulls and mandibles, namely, the type of *C. procar* (A.M.N.H. 234) and C.N.H.M. UC614, a smaller skull and jaw that closely resemble the type

specimen mentioned. Hay (1908) referred this skull to *C. procar* and I am in full agreement with this interpretation.

The remaining four specimens belong to two size classes, juvenile and adult or near-adult. The small individuals are the type specimen of *C. stenopora* and U.S.N.M. 6013, referred to *C. stenopora* by Hay (1909). The larger individuals are A.M.N.H. 6137, a severely crushed skull, a mandible, and a portion of the post-cranial skeleton; the type specimen of *Toxochelys elkader* Hay; and an undistorted, isolated mandible (Y.P.M. 3607).

In an attempt to compare the last four specimens, all of the difficulties alluded to at the beginning of this chapter descend upon the investigator. I have finally concluded, tentatively, that A.M.N.H. 6137 is an adult, or near-adult, individual of *C. stenopora* (there is collateral evidence contained in the plastron) and that Y.P.M. 3607 represents the undistorted mandible of the same species.¹ If this theory should prove to be correct, the mandibles of *C. stenopora* and *C. procar* could be distinguished by a more slender ramus and a distinctly pointed symphyseal tip (fig. 98) in *C. stenopora* and a notable symphyseal ridge on the triturating surface of *C. procar*.

Comparison of the mandibles of *C. procar* and *C. acris* reveals a wider jaw angle in the former species (fig. 98). The lower jaws of *C. tenuitesta* and *C. stenopora* differ in the relative width of the triturating surfaces. These are narrower in *C. tenuitesta* (fig. 98). The described differences are rather slight and quite probably subject to considerable individual variation, but the available material, unfortunately, does not permit a more satisfactory analysis.

Carapace and plastron.—The carapace is elongated and was, probably, rather narrow in life. There is no tendency toward reduction of the peripheral plates. Lateral fontanelles, even in mature specimens, extend continuously from the nuchal plate to the pygal. The neural keel is pronounced and moderately high. The keel elevations are regularly formed by epithecal ossicles whose position coincides with the highest points of vertebral shields 2, 3, and 4. The epineurals are spaced two neural plates apart. An additional epithecal ossicle may occur behind the fourth vertebral shield to form an anal elevation. A preneural element may be present or absent. Circumstantial evidence suggests that where the preneural is apparently absent it is fused to the first neural. Post-nuchal fontanelles are always present. In all cases, the peripheral edge of the carapace is serrated, but the degree and the exact outline of the serrated edge differ individually and between species.

The plastron is difficult to distinguish from that of *Lophochelys*. The hyoploastral suture, as would be expected, increases in length with age, but

¹ Neither the skull nor the mandible is known in the genus *Lophochelys*. The possibility that Y.P.M. 3607 might belong to this genus cannot be disregarded. There is, however, indirect evidence in support of the view here expressed. Y.P.M. 3607 closely resembles the mandible of *C. tenuitesta*. Furthermore, differences in the skull and jaw of members of different genera within this family are on a higher order of magnitude (cf. *Toxochelys* and *Porthochelys*) than those distinguishing Y.P.M. 3607 from *C. tenuitesta* and the other species of *Ctenochelys*.

large lateral and central fontanelles persist. The two Mooreville Chalk species can be distinguished by the shape of the xiphiplastra.

Although a fair amount of vertebrae, girdle, and limb-bones is associated with A.M.N.H. 6137, these elements are so severely crushed that no useful comparisons can be made.

***Ctenochelys tenuitesta* sp. nov.**

Type.—C.N.H.M. P27361, partial carapace and plastron, girdle elements, limb-bones, and vertebrae.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Moore Brothers farm, Harrell Station area, Dallas County, Alabama.

Referred specimens.—Eutaw area, Greene County, Alabama: C.N.H.M. PR30, partial skull roof, braincase, part of snout.

Harrell Station area, Dallas County, Alabama: C.N.H.M. P27354, partial shell; C.N.H.M. PR95, peripheral bones; C.N.H.M. P27404, pygal, peripherals; C.N.H.M. P27362, partial shell, humerus, neurals; C.N.H.M. P27557, hypoplastron, xiphiplastron; C.N.H.M. P27551, hyoplastron; C.N.H.M. P27357, peripheral; C.N.H.M. PR209, peripheral; C.N.H.M. P27481, peripherals; C.N.H.M. P27360, peripherals; C.N.H.M. P27552, shell fragments; C.N.H.M. P27425, peripherals, ulna; C.N.H.M. P27351, partial plastron, scapulae, vertebrae; C.N.H.M. P27429, peripherals; C.N.H.M. P27563, pelvis, peripherals, neurals; C.N.H.M. P27548, partial carapace, pelvis; C.N.H.M. PR248, costals, neurals, peripherals, partial plastron, humerus, vertebrae; C.N.H.M. P27560, peripherals, neurals; C.N.H.M. P27341, mandible; C.N.H.M. P27431, peripherals, coracoid; C.N.H.M. P27402, snout fragment, parietals, mandible; C.N.H.M. P27339, snout fragment, mandible; C.N.H.M. P27558, peripherals, neurals, vertebrae. Specimens tentatively referred to *C. tenuitesta*: C.N.H.M. P27559, shell fragments; C.N.H.M. P27432, shell fragments; C.N.H.M. PR96, shell fragments.

Cedarville area, Hale County, Alabama: C.N.H.M. P27316, partial carapace.

West Greene area, Greene County, Alabama: C.N.H.M. PR161, posterior rim of carapace; C.N.H.M. PR252, xiphiplastra, peripherals, humerus, scapula; C.N.H.M. PR258, mandible, skull fragments, peripherals, partial plastron.

Mt. Hebron area, Greene County, Alabama: C.N.H.M. PR180, peripheral; C.N.H.M. PR24, costals, peripherals, suprapyg, pygal. Specimens tentatively referred to *C. tenuitesta*: C.N.H.M. PR27, peripherals; C.N.H.M. PR57, peripherals; C.N.H.M. PR25, poorly preserved, partial carapace.

Diagnosis.—Skull with elongated snout area; distance between anterior rim of orbit and tip of snout greater than half the width of skull at level of anterior orbital rim. Mandible with slightly concave lateral jaw outline. Peripheral edge of carapace serrated, with individual serrations rounded. Nuchal very wide, moderately concave in front; costo-nuchal sutures nearly transverse. No preneural. Epineural ossicles about half the length of adjoining neurals. A large

upper and small lower suprapygal. Anal elevation formed by an epithecal ossicle overlying lower suprapygal and anterior margin of pygal. Anterior suture of eleventh peripheral not notably oblique. Plastron much longer than wide. Xiphiplastron longer than distance from medial corner of lateral fontanelle to medial, serrated margin of hypoplastron. Xiphiplastron widest at level of keel knob; area behind keel knob relatively long and pointed.

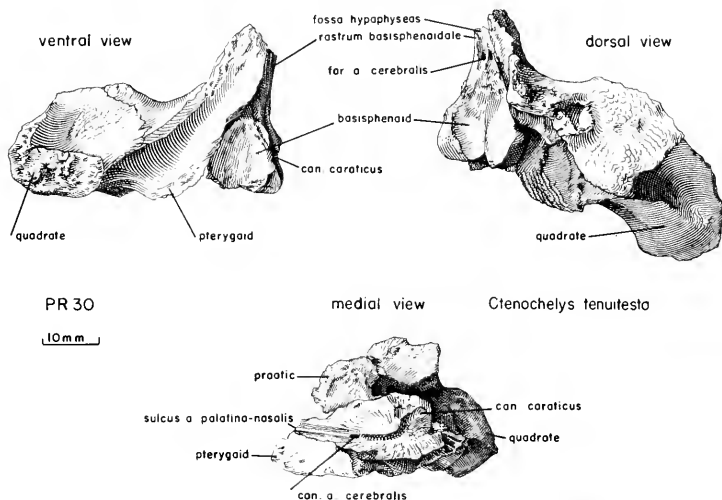


FIG. 100. Fragment of braincase of *Ctenochelys tenuitesta*.

Description.—Five lots of skull fragments are referred to this species. C.N.H.M. P27339 contains a snout fragment of the right side in uncrushed preservation. The ascending maxillary pillar that separates the nostril from the orbit and joins the prefrontal is preserved *in situ* and indicates the relatively great height of the skull in this area. The nostril was certainly higher than wide and the angle between the plane of the nostril opening and that of the palate lies in the vicinity of 60° . Compared with the snout of *C. acris*, that of *C. tenuitesta* is relatively narrower and more pointed. Both nostril and orbit lie relatively farther back (fig. 99). The distance from the tip of the premaxilla to the anterior rim of the orbit measures 45 mm. The antero-posterior width of the maxillary pillar at the narrowest point is 14 mm. The vertical height of the nostril is about 24 mm., measured along the slant about 26 mm. The height of the orbit was approximately 41 mm. The anterior rim of the choanal opening lies 38 mm. back of the tip of the snout. The height of the maxilla below the orbit, at the level of the posterior delimitation of the choanal opening, is about 17 mm., compared to 12 mm. in specimens of about equal size of *C. acris* (C.N.H.M. PR251 and P27337). The mandible of P27339 has, in the horizontal plane, a slightly concave outer masticatory edge. The latter is narrower relative to the

symphyseal length in *C. tenuitesta* than in *C. acris* (fig. 98). Specimen PR30 includes an interesting braincase fragment (fig. 100) that shows the basisphenoid developed in the direction of that of Recent sea turtles (pl. 9), fragments of both maxillae, and a portion of the roof of the skull with one frontal, both parietals and both post-orbitals intact. The dorsal pattern of this section of the skull

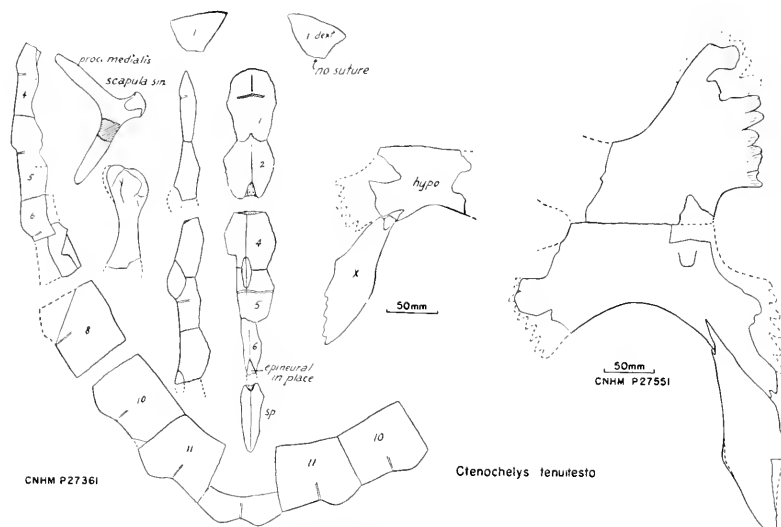


FIG. 101. Type specimen of *Clenochelys tenuitesta* (P27361) and plastron of another specimen (P27551).

roof agrees very well with the corresponding area in *Toxochelys latiremis*. Lot P27402, belonging to a subadult individual, consists of a mandible (fig. 98), a snout fragment and a small portion of the anterior parietal area. The mandible of this specimen is virtually identical in form and size with that of PR258, identified on the basis of the shell remains. An isolated, right mandibular ramus, P27341, agrees closely with the others.

Isolated elements of the vertebral column are associated with five specimens. In P27361 and PR248, the centra of the sixth cervical element have strongly convex joint surfaces posteriorly. The scars to which the neurapophyses are attached reach almost to the mid-line (pl. 20). There is a sharp sagittal ridge at the base of the neural canal, very pronounced in PR248, less so in P27361. Nearly complete eighth cervicals are associated with specimens P27351 and P27548. The centra of these elements are relatively short compared to their width at the narrowest points (see Table 3) but not as short as in *T. moorevillensis* (P27391). The apex of the neurapophysis forms a fairly flat tuberosity that rests against the ventral knob on the nuchal plate; in this as well as in the relative shortness of the centrum, *C. tenuitesta* resembles *Toxochelys* rather than

C. acris. Centra of the ninth (or first shell) vertebra (P27361, PR248 and P27558) are quite massive and ventrally keeled. The neural canal is narrow in front, but widens to more than twice that size posteriorly. In so far as comparison is possible, this element is similar to that in *Torochelys latiremis*. All of the centra of anterior shell vertebrae are ventrally keeled. One of the two caudal

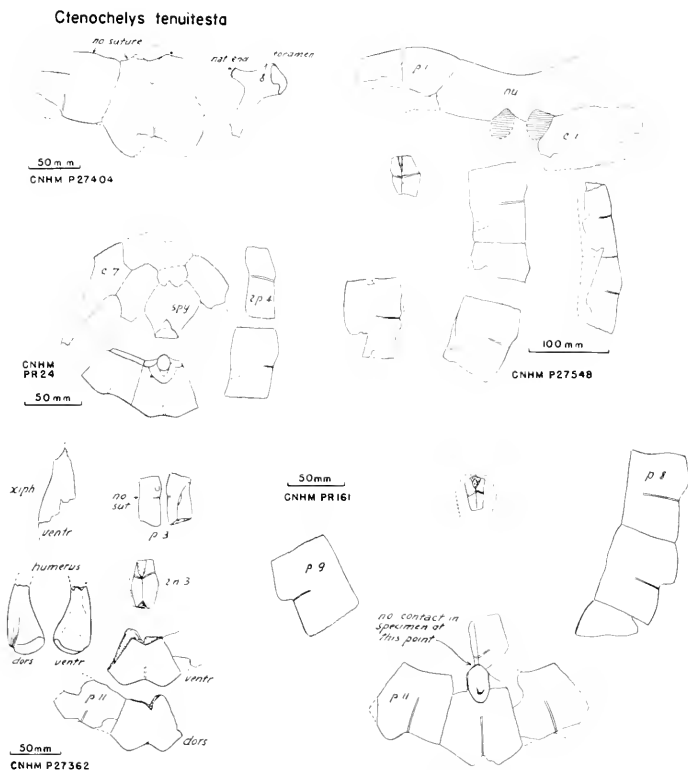


FIG. 102. Referred specimens of *Ctenochelys tenuitesta*.

vertebrae of P27351 is an anterior one; its ribs, standing at right angles to the longitudinal axis of the element, are fused to the transverse processes. The other caudal vertebra belongs to the posterior half of the tail and shows no peculiarities.

The shell material, although represented by a fairly large number of specimens, does not include a single entire carapace or plastron. Since the shell plates are thin, the sutural connections between the different elements were probably weak and easily separated in the process of maceration. Even though this situation is far from ideal, it was possible to work out the basic morphology of the shell and to gain some insight into the range of individual variation, which,

apparently, is great in this species. Most conspicuous is the variable degree of serration on the peripheral bones (figs. 101, 102, 103).

The nuchal is a wide plate, moderately concave in front and acutely pointed laterally. There is a long suture contact with the first costal plates and the sutures run more or less transversely (figs. 102, 104). The first peripheral is without inner suture, which indicates that the nuchal bordered on the lateral fontanelles. There is no preneural. The antero-lateral corners of the first neural form small portions of the rims of the post-nuchal fontanelles. It is a fairly flat plate with a slight keel ridge in its posterior half. All of the following neurals are roof-shaped in cross section. There seem to be two suprapyrgals, as usual in this family, but the upper one is much larger than the lower plate. The latter, present (in a poor state of preservation) only in P27316 (fig. 103), is probably very narrow in uncrushed condition, to judge from the well-defined suture areas on the upper suprapygal and the pygal of PR24. An epithecal ossicle, forming an anal keel elevation at the junction of the suprapygal and the pygal, may have covered the small lower suprapygal entirely. Relatively small epineural elements are located above the contacts of neurals 2 and 3, 4 and 5, 6 and 7 (figs. 101, 104). The peripheral plates are scalloped much as in *Lophochelys*. The degree of serration varies greatly from very slight (P27316, PR24) to very pronounced (P27404, PR161), with the extremes connected by intermediate conditions. The edge of peripherals anterior to the serration point is usually slightly convex, in contrast to *C. acris* in which it is slightly concave. The first peripheral is almost triangular, the inner margin being short. The second peripheral is much wider anteriorly than posteriorly.

The plastron is much longer than wide (fig. 101), thus conforming with the general shape of the carapace. Specimen P27551, an isolated partial plastron, belongs to an unusually large individual. Its xiphiplastron shows the characteristic shape for this species except for the postero-lateral keel knob area, which is severely crushed and presents a definitely exaggerated, angular appearance of the lateral margin. The xiphiplastron of the type specimen (P27361) presents the normal, undistorted outline (fig. 101). The bone is widest at about mid-length, where the keel knob is located, gradually tapering to a point posteriorly. Slight serrations are visible along the medial edge.

In the shoulder girdle, the scapula is all but indistinguishable from that of *Toxochelys*, but entirely complete elements are not known. The two scapular processes are subequal in length, the dorsal, as usual, being the longer. In P27404 (fig. 102), the ?ventral process is abnormally short and there is a foramen that pierces the neck of the bone in approximately an antero-posterior direction. A foramen of this sort was not observed in any other specimen. This bone is so unusual that it is difficult to determine whether it is a right or a left scapula. The coracoid shows considerable distal expansion, probably not much exaggerated in the specimen illustrated (fig. 106). The humerus (fig. 106) lacks the distal end. Its ulnar process is crushed toward the main shaft of the bone. The proximal end of another humerus (PR248) is somewhat flattened in the plane of the

ulnar process and consequently presents quite a different appearance. Because of these difficulties, detailed descriptions of these bones are of doubtful value.

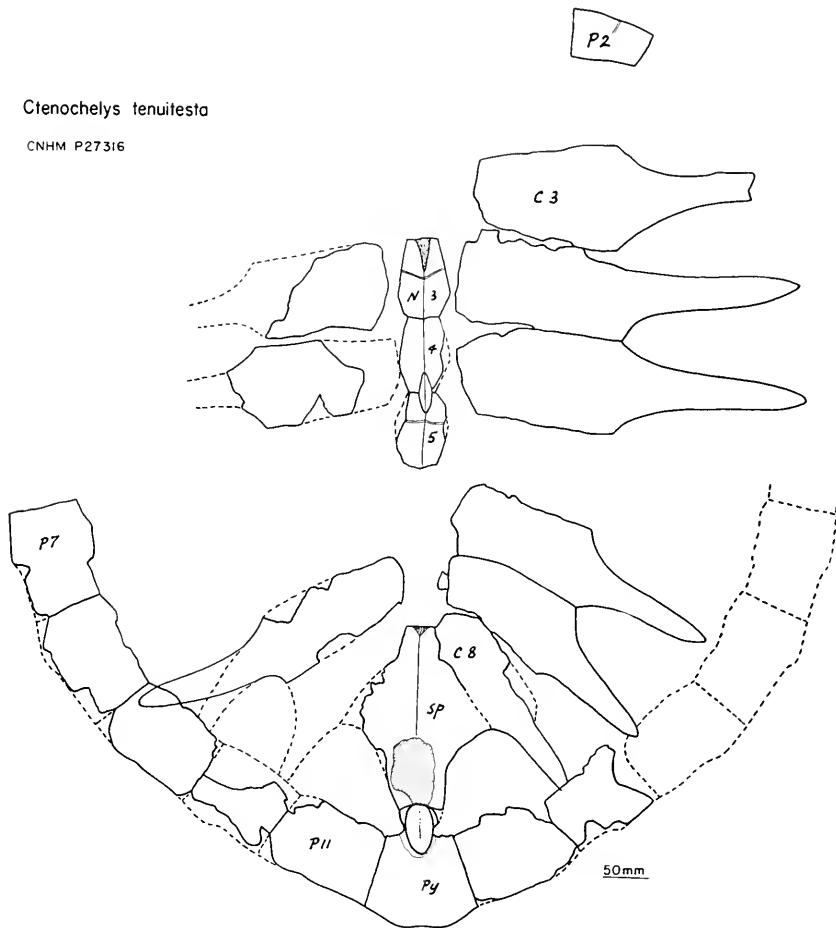


FIG. 103. Referred specimen of *Ctenochelys tenuitesta*.

Of the pelvis, the pubis is represented in a fragmentary condition only. The right ilium and the left ischium (PR248) are shown in fig. 106. The angle between the axes of the vertical shaft and the postero-dorsal process of the ilium is about 110° . A well-preserved left ilium is associated with P27425, a specimen with unusually weak peripheral serration. The dorsal half of the shaft of the ilium is concave on the medial side, but the surface bone is not as rough as, for example, in the Recent *Macrochelys*. On the lateral side of the bone, there is a

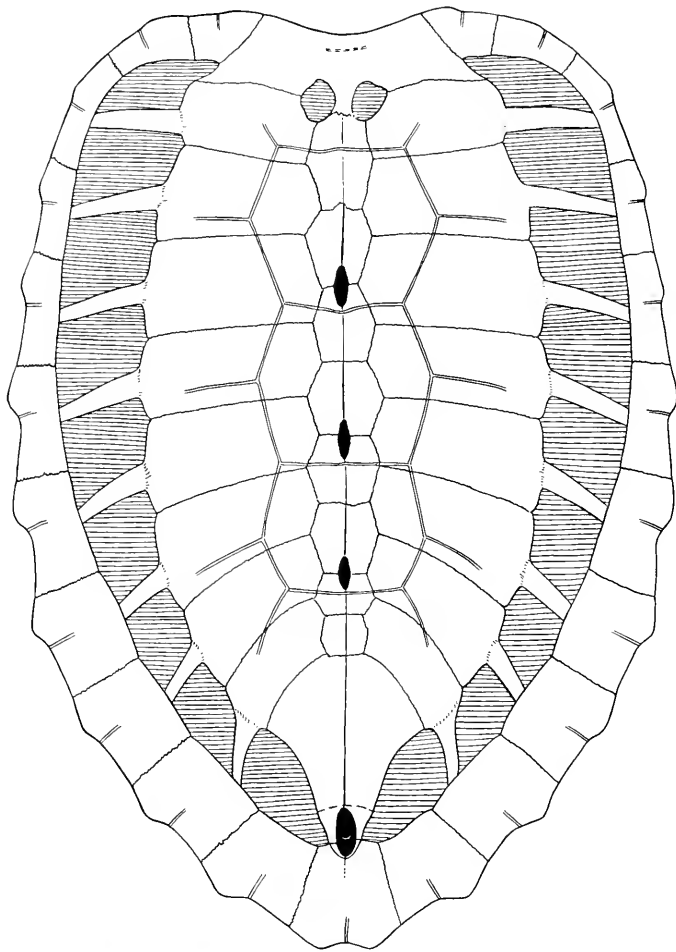
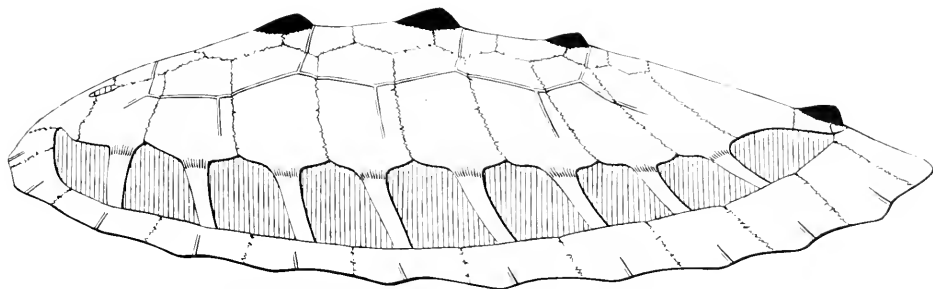
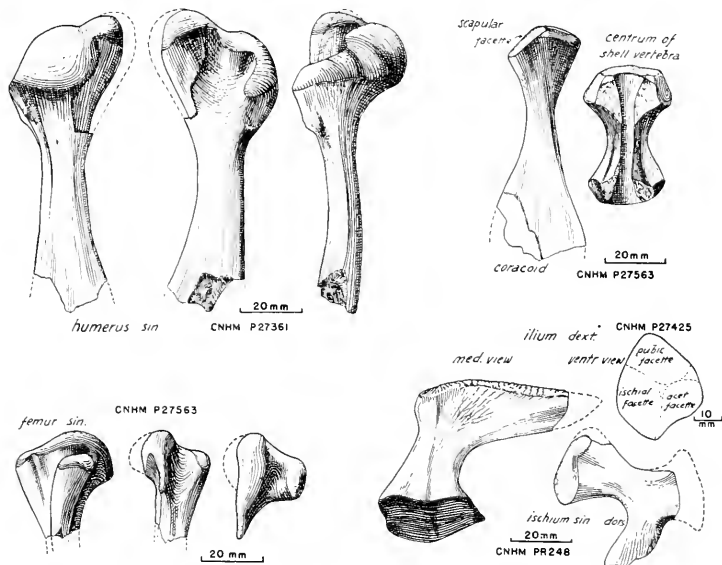
Ctenochelys tenuitesta

FIG. 104. *Ctenochelys tenuitesta*. Reconstruction of carapace based on all available materials.

corresponding convexity whose surface is sculptured with many parallel ridges. The postero-dorsal process ends with a clearly delineated, slightly concave, smooth area. The ventral end of the bone shows clearly the ischial and pubic attachment surfaces and the concave ilial component of the acetabular cavity (fig. 106).

The postero-lateral process of the ischium is short and stout, less than half the medio-lateral width of the bone (fig. 106). Only the proximal end of the

Ctenochelys tenuitestaFIG. 105. *Ctenochelys tenuitesta*. Reconstruction of carapace in side view.*Ctenochelys tenuitesta*FIG. 106. Girdle and limb elements of *Ctenochelys tenuitesta*.

femur is known (P27563). In the present state of our knowledge, it is not distinguishable from that of other toxochelyid turtles (fig. 106).

***Ctenochelys stenopora* (Hay)**

Toxochelys serrifer Case (non Cope), Univ. Kansas Geol. Surv., 4, p. 379, pl. 80, figs. 3-9, pl. 82, figs. 4, 5, pl. 83, fig. 1, 1898; Hay, Amer. Nat., 32, p. 935, figs. 1-3, 1898; U. S. Geol. Surv. Bull., 179, p. 442 (in part), 1902; Williston, Trans. Kansas Acad. Sci., 17, p. 198, 1901.

- T. stenoporus* Hay, Bull. Amer. Mus. Nat. Hist., **21**, p. 180, figs. 8-12, 1905.
T. stenopora Hay, Carnegie Inst. Wash. Publ., **75**, p. 172, figs. 214-220, 1908; Proc. U. S. Nat. Mus., **36**, p. 191, pl. 5, text fig., 1909.
T. bauri Wieland, Amer. Jour. Sci., **20**, p. 325, pl. 10, figs. 1-8, 1905; Hay, Carnegie Inst. Wash. Publ., **75**, p. 178, figs. 229, 230, 1908.
T. procar Hay, Carnegie Inst. Wash. Publ., **75**, p. 176, fig. 227, 1908.
T. elkader Hay, Carnegie Inst. Wash. Publ., **75**, p. 174, figs. 221-223, 1908.
Toxochelys sp. Hay, Carnegie Inst. Wash. Publ., **75**, p. 164, pl. 30, 1908.

Material.—See below.

Amended diagnosis.—Skull with slender snout region. Triturating surfaces narrower than distance between them near posterior end. Mandible pointed in front; symphyseal ridge on triturating surface weak or absent. Carapace oval with large lateral fontanelles, equaling or exceeding in width the lateral extent of the adjoining costal plates. Peripheral edge serrated as in *C. tenuitesta*. Nuchal moderately concave in front. Costo-nuchal sutures slanting forward and outward. Epineural ossicles more than half the length of adjoining neural plates. Position of epineural ossicles apparently somewhat variable. No epithecal anal elevation. Large upper and small lower suprapygal. Anterior suture of eleventh peripheral not notably oblique. Plastron wider than long; length of xiphiplastron equal to distance between medial corner of lateral fontanelle and medial, serrated edge of hypoplastron.¹ Xiphiplastron widest at level of keel knob; area behind keel knob short.

Discussion.—The type material of this species appears to have suffered from repeated, somewhat inadequate, curatorial care in the past. At the time of Hay's (1908) redescription of the specimen, some of the bones that were quite probably associated when Case (1898) rendered the first description of it bore different collection numbers, namely, 2060 for the skull, peripherals, and hyoplastron, 1270 for the hypo- and xiphiplastron, neurals, suprapygal, and costal plates. Today, a specimen bearing the number K.U. (V.P.) 1205 (fig. 108) consists of the same posterior carapace bones that appear on Case's plate 83 (op. cit.). The similarity is such that there is no doubt that it was the specimen studied by Case. In fact, there is no good reason to suspect that different individuals or even species are contained among these materials. The size of the skull fragment relative to the width of the hyoplastron agrees closely with the comparable parts of specimen U.S.N.M. 6013, a juvenile of about the same size. While there is little doubt there is likewise no ultimate proof that the skull fragments were associated with the shell bones. Since Hay (1908, p. 173) designated especially the skull as the name-bearer of the species, the question of the association of the type material is, in so far as this case is concerned, of interest and importance, because the skulls are much more difficult to identify than are the shells. The relatively great number of skulls of *Toxochelys latiremis* gives an

¹ This is a peculiar correlation that applies to both juvenile and adult individuals (4 specimens tested).

idea of the effect of post-mortem changes that alter the appearance of skulls to such an extent that they may appear entirely dissimilar in very many respects.

Hay (1909) described the juvenile slab specimen U.S.N.M. 6013, of nearly the same over-all size as the type, and referred it to this species. Another specimen (A.M.N.H. 6137), of which only the skull and mandible were prepared at

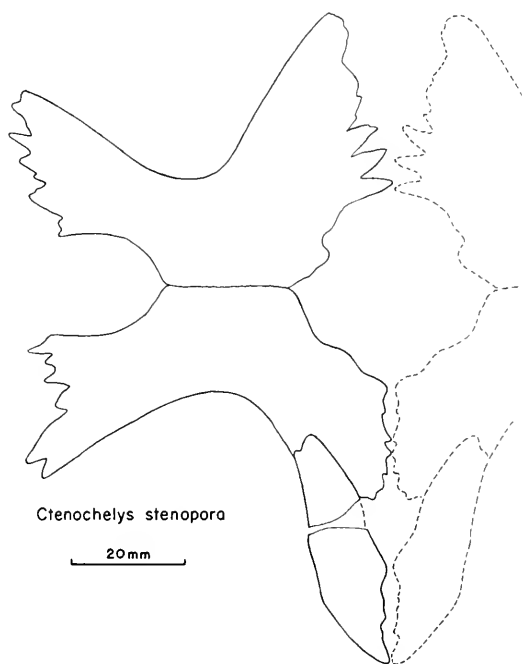


FIG. 107. Plastron of *Ctenochelys stenopora*. After Case and Hay.

the time, was made the type of *Toxochelys elkader* by Hay (1908). The skull, severely compressed dorso-ventrally, differs in a number of features from the type of *C. stenopora*, particularly in the illustrations rendered by Hay. The post-cranial skeleton, on the other hand, belongs to this species without doubt. Since there is no doubt as to the association in A.M.N.H. 6137, one might suspect that the skull of the type material of *C. stenopora* does not belong with the shell. There is, however, no doubt as to the association of skull and shell in U.S.N.M. 6013, and the skull of the latter compares quite well with that of the type. The differences between the skulls of A.M.N.H. 6137 on the one hand and the type skull and U.S.N.M. 6013 on the other are thus probably due to differences in preservation and in age, since A.M.N.H. 6137 is an adult or near-adult individual.

In addition to the three specimens mentioned, the fairly complete shell, Y.P.M. 1786, described as *Toxochelys bauri* (Wieland, 1905), an undescribed

juvenile skeleton, U.S.N.M. 12009, from the Niobrara Chalk, 2 miles south of Russell Springs, Kansas, an isolated mandible, Y.P.M. 3607, a specimen, K.U. (V.P.) 1228, described and figured by Hay (1908, p. 164, pl. 30) but not specifically identified, and a juvenile plastron, C.N.H.M. UR2, are here referred to *C. stenopora*.

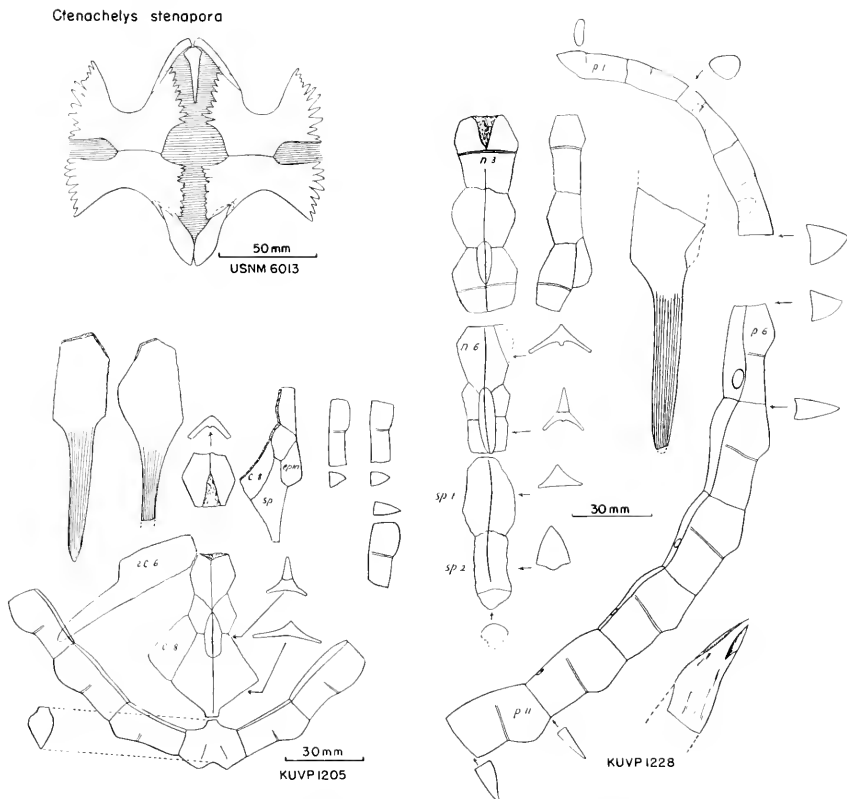


FIG. 108. Plastron and fragments of carapace of *Ctenochelys stenopora* (juvenile). After sketches and photographs of originals.

The type specimen of *Toxochelys bauri*, Y.P.M. 1786, and K.U. (V.P.) 1228 (fig. 108) resemble each other fairly closely except in size. Both differ from K.U. (V.P.) 1205 notably in the posterior neural series and the suprapygal region. It is, indeed, doubtful that a difference of this magnitude can be assumed to represent extremes in individual variation, although deviations from the normal pattern of even greater scope can be observed rather frequently in Recent emydid turtles. It might be suggested that these two shells belong to *C. procar*, of which no associated shell material is known. This remains a possibility, of

course. I have chosen to include the two specimens in question under *C. stenopora* for a number of reasons, none of which are, however, conclusive. The species *C. procax* appears to be rare, only two skulls being definitely known. In view of

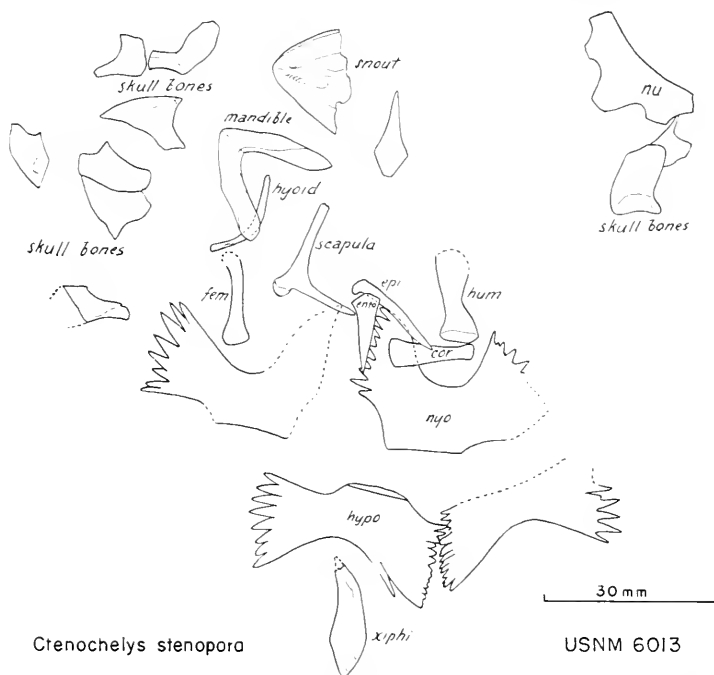


FIG. 109. Tracing of part of slab specimen of *Ctenochelys stenopora* (U.S.N.M. 6013, juvenile).

the similar situation in the Mooreville Chalk, it appears unlikely that there are more than two species of *Ctenochelys* represented in the Niobrara beds. The Mooreville species, *C. tenuitesta* and *C. acris*, differ from each other throughout their known anatomy, not merely in one area of the shell. In so far as can be determined, *C. tenuitesta* and *C. stenopora*, on the one hand, and *C. acris* and *C. procax*, on the other, are the most closely related species. No shell material from the Niobrara was noticed that was similar to that of *C. acris*. All of this is indirect evidence and in no way proves the case. Additional material is required to clarify the matter.

The features of the skull and mandible of this species had to be discussed in the general account of the genus. Comparison of the shell materials here referred to *C. stenopora* with those of *C. tenuitesta* reveals the great over-all similarity between these forms. The plastra are wider than long, however, indicating that *C. stenopora* has either a more broadly oval shell or relatively

shorter anterior and posterior plastral lobes, leaving a relatively greater area of the ventral surface unarmoured. The peripherals are indistinguishable from those of *C. tenuitesta*. The nuchal plate is moderately excavated in front as in *C. tenuitesta*, but the costo-nuchal sutures slant forward and outward as in *C. acris*.

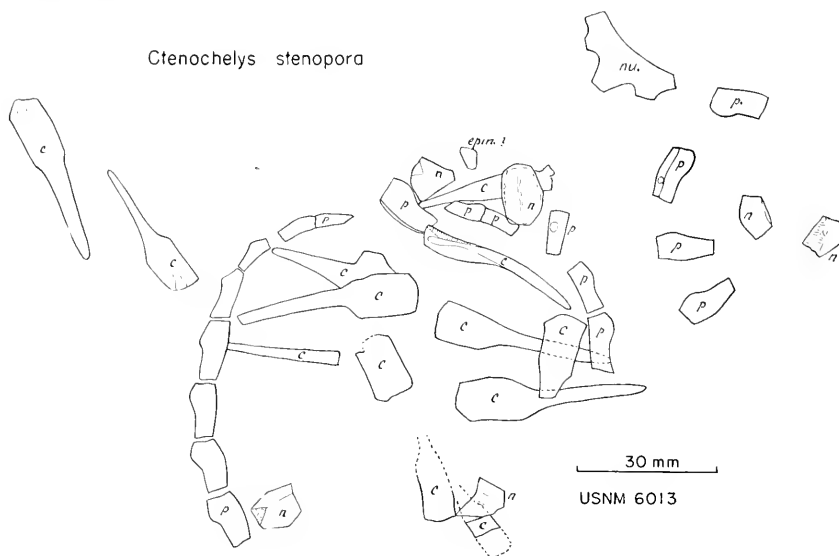


FIG. 110. Tracing of part of slab specimen of *Ctenochelys stenopora* (U.S.N.M. 6013, juvenile).

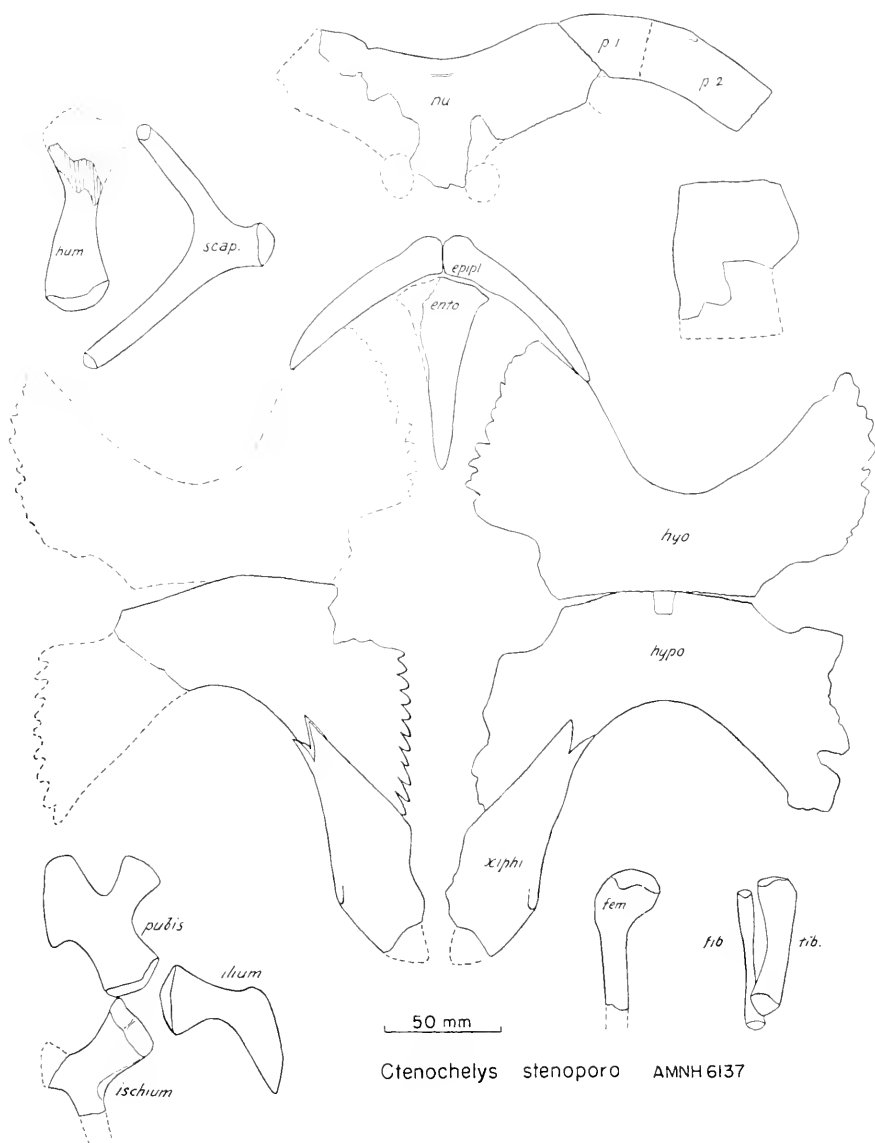
The neural keel elevations are as pronounced as those of *C. acris*. The plastron of A.M.N.H. 6137 is complete except for the right hyoplastron (fig. 111). The epiplastra are thin, narrow plates of typical toxochelyid shape. The entoplastron is very thin and twice as long as wide anteriorly. The central fontanelle extends forward to the epiplastra. The xiphiplastra are widest at the level of the keel knob; the area back of this point is short and bluntly pointed. The shape of this element is thus intermediate between that of *C. tenuitesta* and *C. acris*.

The girdle and limb-bones of A.M.N.H. 6137 are entirely flattened. The outlines of some of them retained recognizable features and are illustrated (fig. 111). The proportions of the scapula are almost identical with those of *Lepidochelys kempi* (see Table 5).

***Ctenochelys acris* sp. nov.**

Type.—C.N.H.M. P27354, partial carapace, plastral fragments.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Moore Brothers farm, Harrell Station area, Dallas County, Alabama.



Ctenochelys stenopora AMNH 6137

FIG. 111. *Ctenochelys stenopora* (A.M.N.H. 6137). Most significant parts of skeleton associated with skull described by Hay as *Toxochelys elkader* (see pl. 17).

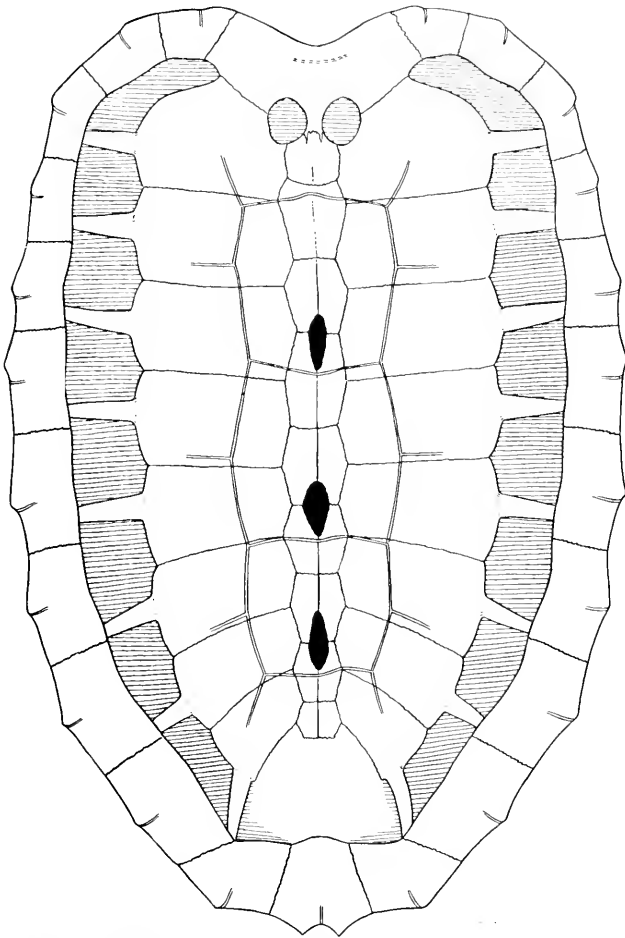
Ctenochelys acris

FIG. 113. *Ctenochelys acris*. Reconstruction of carapace from all available materials.

Peripheral edge of carapace with small but acute individual serrations located almost directly at shield furrow in posterior peripherals. Nuchal deeply concave in front; costo-nuchal sutures slanting forward and outward. A preneural. Epineural ossicles more than half as long as adjoining neurals. No anal elevation. Anterior suture of eleventh peripheral notably oblique. Plastron insufficiently known. Xiphiplastron equals distance between medial corner of lateral fontanelle and medial serrated margin of hypoplastron. Xiphiplastron widest across posterior third, blunt posteriorly.

Description.—This appears to be a relatively rare species. The materials on which the description is based belong to very fragmentary specimens and much information is still wanting. If it were not for the fact that the turtle shell exhibits a fairly stable pattern in its arrangement of parts, it would surely not be possible to give a reconstruction of this animal (fig. 113) at present. It may be noted at the outset that while the two forms (figs. 104 and 113), seen as morphological entities, clearly show distinct features, many single characters of this species are also present in *C. tenuitesta*. It is thus not always possible to identify fragmentary specimens without access to the entire present collection.

Specimen P27337 represents the best skull material so far collected. It consists of the braincase, the snout area, a portion of the roof, and the mandible, lacking the posterior end on the right side. The snout fragment (pl. 18) conforms both in size and shape to PR251. Both specimens are characterized by relatively short snouts as compared with *C. tenuitesta* (fig. 99). In both of these individuals, furthermore, the maxilla is notably thinner in dorso-ventral direction at the base of the ascending maxillary pillar than in *C. tenuitesta*. The braincase fragment of P27337 resembles that of *C. tenuitesta* (PR30, fig. 100) in the sense that the basisphenoid rostrum approximates the condition in Recent chelonid turtles. On the ventral side of the fragment, there is a deep depression in the forward area of the basioccipital, framed by the basisphenoid ridges, which is also seen in P27340. Severe crushing appears to have made these depressions more conspicuous. The mandibles are broadly rounded in front, not pointed as in *C. tenuitesta* (fig. 98). A well-preserved jaw (P27366) shows a notable symphyseal ridge, sharpest at mid-length.

An isolated, well-preserved, eighth cervical vertebra (PR137) shows two characters of interest. The centrum is about twice as long as wide at its narrowest point and nearly the same proportion is seen in the fairly well-preserved eighth cervical of PR97 (width 53 per cent of length). The high neurapophysis does not form a flat tuberosity at its apex, which, in other toxochelyid turtles, rests against the ventral knob on the nuchal plate. Instead, it is medially divided by a deep sulcus. Specimen PR97 shows exactly the same situation. The additional three cervical vertebrae of PR97 are so badly distorted that their numerical position in the column cannot be definitely determined. The two posterior sacral and the first caudal vertebrae (PR97) are preserved intact. All three elements have ventrally keeled centra, but these ridges are blunt. The last sacral rib is larger than the second, as in *Toxochelys*. A sixth cervical centrum (P27354) is virtually indistinguishable from its homologue in *C. tenuitesta*. Two centra of anterior shell vertebrae are acutely keeled ventrally. Five caudal vertebrae (P27352) belong to different parts of the tail series. These vertebrae, as those of *Toxochelys*, are procoelous and relatively broader, not laterally compressed as are those of *Chelydra*, but resemble them rather closely otherwise. They may or may not have borne dermal ossicles. Small haemapophyses of chelydrid shape are present on one of the vertebrae.

The carapace was probably long and narrow. The nuchal plate is deeply concave anteriorly and forms but a short suture with the first costal, which slants

sharply forward and outward. There is no ventral anchor knob for the eighth cervical vertebra. In the type specimen (P27354) and in PR62, preneural elements are developed. The first neural is thus traversed by the vertebral shield furrow near its anterior end, not near the middle as in *C. tenuitesta* (figs. 112 and 113). In *C. acris*, the epineural ossicles are relatively larger than in *C. tenuitesta*; their length exceeds half the length of the adjoining neural plates. The suprapygal region is not known, nor is the pygal. But the approximate shape of the pygal is largely determined by the peculiarities of the eleventh peripheral (fig. 112). The anterior suture contact of the latter with the tenth peripheral is unusually oblique, and determines its approximate position relative to the shell as a whole. The marginal edge of all of the posterior peripherals exhibits a feature characteristic of this species, namely, a type of serration in which the edge anterior to the serration point of each peripheral is slightly concave; the point itself is small but acute and located immediately in front of the scale furrow or directly at the spot where the shield furrow reaches the margin (fig. 112). The marginal edge of the anterior peripherals (1-6) is not distinguishable from that of *C. tenuitesta*. The nuchal suture of the first peripheral is less oblique in this species than in *C. tenuitesta* and the second peripheral is of nearly equal width anteriorly and posteriorly, whereas in *C. tenuitesta* there is a considerable difference (figs. 104, 113).

The plastron is not satisfactorily known. The xiphiplastron (fig. 112), however, is readily distinguishable from that of *C. tenuitesta* since it is widest in its posterior third, rather than at mid-length.

Most of the girdle and the limb-bones are so incompletely preserved that they are difficult to compare. Of the two scapulae, P27352 and PR137, the former has a more elongated neck region than that of any other known toxochelyid scapula. Specimen PR137 is indistinguishable from *C. tenuitesta*. Neither of these specimens has complete processes. The coracoid (PR137), lacking the posterior end, cannot be distinguished from *C. tenuitesta*.

Ctenochelys procax (Hay)

Toxochelys procax Hay, Bull. Amer. Mus. Nat. Hist., **21**, p. 181, figs. 13, 14, 1905; Carnegie Inst. Wash. Publ., **75**, p. 176, figs. 224-226, 1908.

Type.—A.M.N.H. 234, large skull and partial mandible.

Horizon and locality.—Niobrara Chalk. Kansas.

Referred specimens.—See below.

Amended diagnosis.—Skull with wide, broadly rounded snout area. Width of triturating surfaces greater than distance between them near posterior end. Mandible not pointed in front. A notable symphyseal ridge forming a broad convexity near posterior end of symphysis. Width of triturating surface relative to length of symphysis conspicuously greater than in other species of the genus. Post-cranial skeleton unknown.

Discussion.—The type of this species is a large skull and partial mandible, A.M.N.H. 234. Another skull with mandible of somewhat smaller size (C.N.H.M.

UC614, formerly UC572) resembles the type so closely in every respect but size that the identification is in no doubt. The isolated jaw fragment K.U. (V.P.) 2050, referred to this species by Hay (1908), is badly crushed and cannot be identified as to species. The mandibular fragment A.M.N.H. 220, also referred to *C. procar* by Hay (1908), compares more closely with Y.P.M. 3607 and is thus referred to *C. stenopora*. There are no shell materials associated with the type or with C.N.H.M. UC614. Concerning the possible reference of shell specimens to this species, see discussion under *C. stenopora* (p. 240).

Prionochelys gen. nov.

Characterization.—Highly specialized genus. Skull with lophochelyine palate and epidermal shield cover. Carapace cordiform, with deep peripheral serrations and pronounced excavation of anterior nuchal rim. Neural carina, consisting of ten elements, one preneural and nine neurals, very high; contains epithecal elements located at junction of neurals 2 and 3, 5 and 6, 8 and 9. Nuchal plate much wider than long. First peripheral plates encroach upon nuchal laterally. Preneural much wider than long. No post-nuchal fontanelles in adults. Plastron poorly known. Xiphiplastra similar to those of *Ctenochelys*.

Type of genus.—*Prionochelys nauta*.

Horizon and locality.—Marlbrook Marl, Late Cretaceous. Arkansas.

Discussion.—*Prionochelys* occurs in both the Mooreville Chalk of Alabama and the Niobrara Chalk of Kansas. The best materials, however, come from the Marlbrook Marl of Arkansas, which represents a notably higher stratigraphic level. All of the Marlbrook specimens are large, but there is evidence that the older Mooreville form was an equally large turtle. *Prionochelys* is apparently very rare in both the Mooreville Chalk and the Niobrara, whereas in the Marlbrook Marl it would seem to be the dominant form.

In so far as comparison is possible, it can be stated that *Prionochelys* possessed a typical toxochelyid skull. The palate was of lophochelyine character, with a large portion of the palatines forming the medial edges of the masticatory surfaces on either side of the choanae. The roof of the skull was covered with epidermal shields. The articular surfaces of the quadrates consist of large medial and small lateral facets.

The features of the carapace are outstanding. The neural elements (a preneural and nine neurals) form a high keel with four or five dorsal elevations, namely, a cervical (above preneural), a pectoral, an abdominal and a pelvic; an anal elevation may be located at the junction of the suprapygal and pygal plates (fig. 114). The pectoral, abdominal and pelvic elevations may be formed either by epithecal elements only (as in *Ctenochelys*) or by neural plates in conjunction with epithecal. The latter are always spaced three neurals apart, instead of two as in *Ctenochelys*. Among the three recognized species, there are considerable differences in the detail of keel specialization (fig. 114).

The peripherals are deeply serrated, with the serration points at, or near, the suture of adjoining elements. Lateral fontanelles are always present. Post-nuchal fontanelles are seen in *P. galeotergum*, absent in *P. nauta*. Since the only known specimen of the former is a young individual, whereas the latter is based on large material only, the presence or absence of post-nuchal fontanelles in this genus might well be a matter of age rather than a specific difference.

No suprapygal plates are known. It is possible that there is only one, the lower one. The upper suprapygal of the generalized toxochelyid shell appears to have become segmentally displaced into the position of neural 9 in this genus, thus assuming the role and the shape of that element.¹

The plastron is incompletely known. It is typically toxochelyid, however, and the xiphiplastra are very similar to those of *Ctenochelys*.

Of the girdles, only the ilium and ischium are known. They are practically indistinguishable from those of *Toxochelys*. The limbs are unknown.

***Prionochelys nauta* sp. nov.**

Type.—C.N.H.M. P26237, partial shell, neurals, peripheral fragments, costals, and fragments of plastron.

Horizon and locality.—Marlbrook Marl, Late Cretaceous. Devil's Backbone, Saratoga, Howard County, Arkansas.

Referred specimens.—C.N.H.M. P26238, partial carapace and plastron (Devil's Backbone, see above); C.N.H.M. PR271, fragment of plastron (same locality as above); C.N.H.M. P27456, peripherals, plastral fragment (Nick Gaiter farm, ca. 1 mile northeast of junction of Okolona-Hollywood road to Arkadelphia, Clark County, Arkansas; Marlbrook Marl); C.N.H.M. P27461, partial carapace, skull fragments (same locality as P27456); C.N.H.M. PR221, nuchal and first peripheral (same locality as P27456); C.N.H.M. P27460, fragmentary specimen (same locality as P27456); C.N.H.M. P27454, partial carapace and plastron (Cox farm, same data as P27456).

Diagnosis.—Spectacular turtles. Carapace with specialized neural keel and high cervical, pectoral, abdominal, and pelvic elevations. Epithecal ossicles large. Ridge line of neural 2 as long as distance between anterior and posterior sutures. Neural 8 short, almost excluded from the ridge profile. Preneural with antero-lateral wings; no post-nuchal fontanelles in adult. Shell thick. Xiphiplastron widest at level of keel knob.

Description.—The only skull material, consisting of fragments that cannot be fitted together, is associated with P27461. The identifiable pieces include a portion of the right mandible, portions of both maxillae with parts of the palatine bones suturedly attached, the left ascending ramus of the maxilla with part of the prefrontal in place, a portion of the roof of the skull in the area of the junction of the frontal, parietal, and post-orbital bones, a fragment of the left otic

¹ For comparable examples of segmental displacement of serial structures, see Kühne, 1936; Schinz and Zangerl, 1937.

area, and the articular processes of both quadrates. The mandible is represented by three disconnected sections from the masticatory region.

These fragments belong to a skull of the approximate size of that of a large *Caretta*. The suture pattern of the bones of the skull roof resembles closely that of other toxochelyid turtles; the frontal bones form the dorsal edges of the

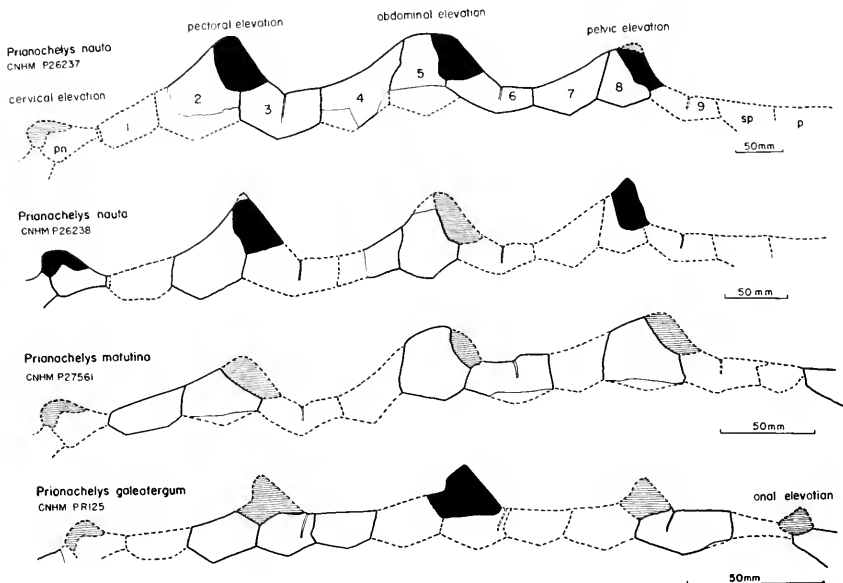


FIG. 114. Comparison of morphology of keel in *Prionochelys nauta*, *P. matutina*, and *P. galeotergum*.

orbits. The skull was covered with epidermal shields. The interorbital bridge at the fronto-parietal junction is 76 mm. wide. Fragments from either side of the choanal opening show the maxillo-palatine suture. The palatine bones formed a considerable portion of the triturating surface; it is not possible, unfortunately, to determine whether the condition is similar to that of *Ctenochelys* or further advanced in the direction of secondary undershelfing of the choanal passages. The alveolar ridge is relatively low, about the same relative height as in *Ctenochelys*. The articular processes of the quadrates show articular joint surfaces characterized by large medial and small lateral facets, separated from each other by longitudinal elevations, thus differing from those of *Toxochelys* and *Ctenochelys* in which the lateral facets are larger and are separated from the medial facets by longitudinal depressions (fig. 115). The mandible seems very massive. The fragments permit the statement that it is, in general organization, similar to that of *Ctenochelys*. The triturating surface may be relatively wider than in the latter genus, but it was certainly not expanded as in *Osteopygis*.

The carapace (fig. 116) does not reach the degree of ossification illustrated in the reconstruction until the individual has attained the size of the largest specimens now under study. In P26238, an individual somewhat smaller than the rest, the lateral fontanelles extend forward to the nuchal plate and the first peripheral is thus relatively long and narrow (pl. 28). In the largest specimens

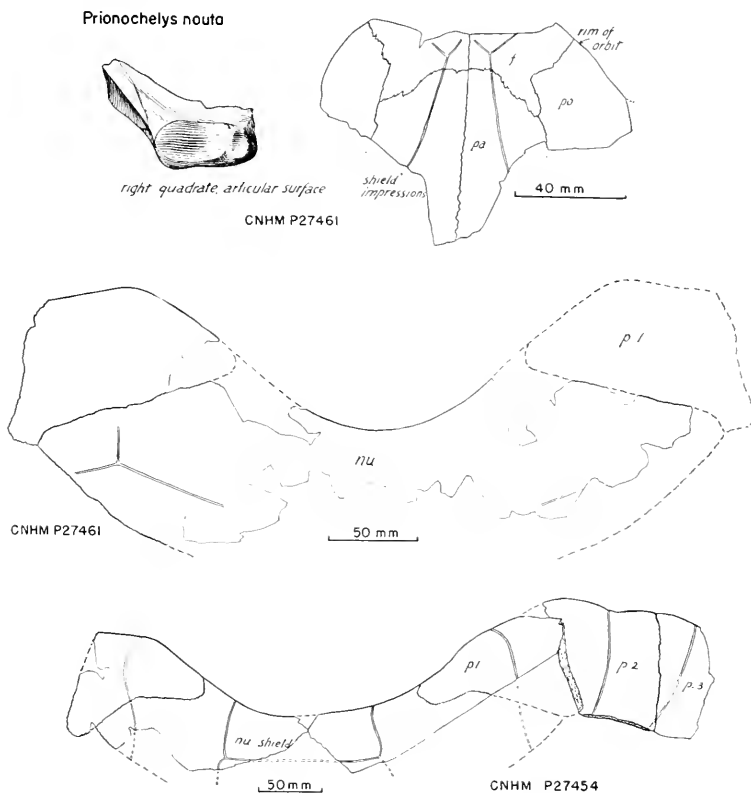


FIG. 115. Skull fragments and portions of anterior carapace of *Prionocheilus nauta*.

(P27461 and P27454, fig. 115), the lateral fontanelles extend forward approximately to the junction between peripherals 2 and 3. The first peripheral is, at this stage, triangular in shape. Clearly, the rate of ossification progresses at a faster pace than the general growth of the individual at these rather late ontogenetic stages. There is no indication in any specimen that the lateral fontanelles disappear entirely.

The nuchal plate, in the fully developed condition, is a wide plate, pointed laterally and excluded from the rims of the lateral fontanelles (figs. 116, 117).

It is deeply excavated in front and forms an unusual suture contact with the preneural (pl. 28). It is probable that post-nuchal fontanelles are present in the young, but this remains to be demonstrated in future discoveries.

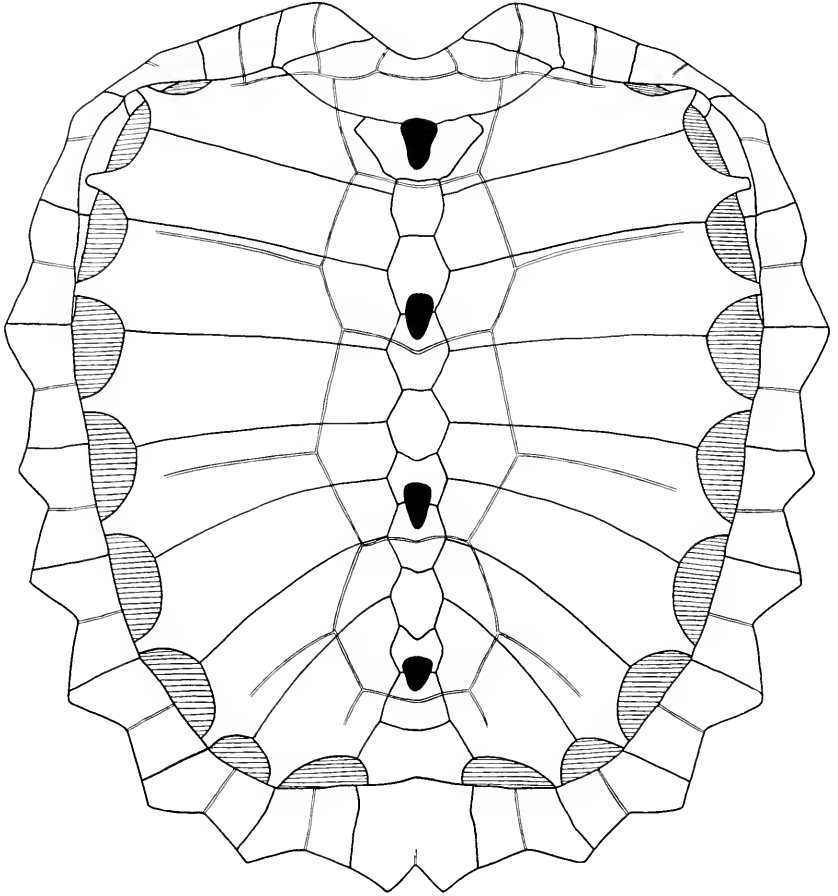


FIG. 116. *Prionocheilus nauta*. Reconstruction of carapace from all available materials.

The neural series of this form is the most advanced of the three known species. Between the two specimens P26237 and P26238, the preneural and eight thecal neurals are known; a ninth, bearing a transverse shield furrow and resembling in type neurals 3 and 6, must have followed neural 8 (the ninth neural is known in *P. matulina* and *P. galeotergum*). The thecal neural elements form part of the keel profile and have thus become greatly modified. Four dorsal keel elevations in cervical, pectoral, abdominal, and pelvic positions are documented

in *P. nauta*. The cervical elevation is formed mostly by an epithecal ossicle located at the junction of the nuchal plate and the preneural. Three neural plates and one epithecal ossicle each contribute to the formation of the pectoral, abdominal, and pelvic elevations. Neurals 1, 4, and 7, neurals 2, 5, and 8, and neurals 3, 6, and 9 are of essentially similar shape and are in comparable positions relative to the apices of these elevations. There is, however, a progressive crowding of the neurals from the pectoral to the pelvic elevation, affecting primarily neurals 2, 5, and 8. In the pectoral elevation, neural 2 forms the ascending component of the apical profile. Neural 5 in the abdominal elevation has a short

Prionochelys nauta

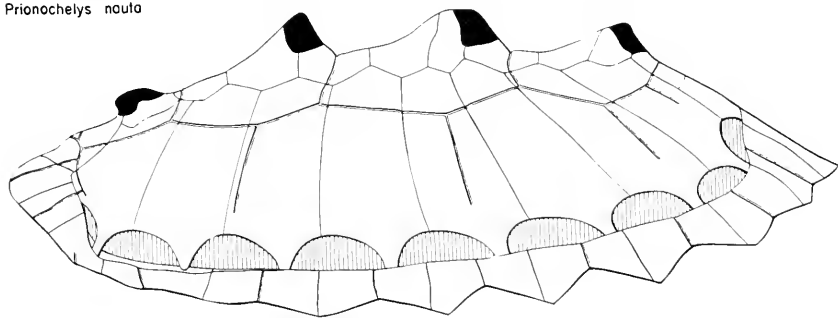


FIG. 117. *Prionochelys nauta*. Lateral view of reconstructed carapace.

ridge line and forms the apex proper. Neural 8 is the central element of the pelvic elevation; it is, however, short and all but excluded from the apical profile (fig. 114; pl. 27).

The keels of P26237 and P26238 show minor differences probably correlated with the size difference between the two specimens. In the smaller individual (P26238), the ridge line of the keel is sharper and the apices are more acute. The fourth neural in the abdominal elevation does not reach to the apex as it does in the larger individual; it resembles the more primitive condition in *P. matutina* (fig. 114).

The costal plates, of which numerous fragments but only a few nearly entire elements are available, are rather thick (± 10 mm. along the sutures of the costals illustrated in pl. 27) and the ribs are not clearly distinguishable from the overlying plates, as is always the case in the other toxochelyid genera. A fair number of proximal costal fragments, on which shield furrows are deeply impressed, permit a reasonably accurate reconstruction of the vertebral and pleural shield pattern (figs. 116, 117).

The peripheral plates, like the rest of the carapace, are relatively massive. Of P27456, a moderate-sized individual, only peripherals and a piece of plastron were preserved. The lot contains peripherals 3, 8(?), 10, and 11 of the right side (pl. 29) and 8(?) and 11 of the left side. The marginal edge is deeply notched and sharp. The elements attain their greatest width directly behind or at the

sutural contacts with the preceding peripherals (pl. 29 and fig. 116). The anterior suture plane of the eleventh peripheral stands at an oblique angle to the longitudinal axis of the element, resembling the condition of *Ctenochelys acris* (fig. 113). The medial faces of the peripherals are slightly concave and rather smooth. Distinct but shallow rib-pits are present on the third and on the extreme posterior end of the tenth peripherals. On the eighth(?), there is no trace of a pit, but the dorsal half of the medial face, overlying the rib end, shows a slight impression half way between the shield furrow and the posterior suture. The dorsal edge of the medial face of the peripheral is thick and blunt throughout its length, except at the place where it overlay the rib; there it is much thinner and sharper. The dorsal surfaces of these peripherals are slightly convex in medio-lateral direction, a matter likewise true in the other species of *Prionochelys*, but not in any other toxochelyid genera where the dorsal surface of the peripherals is more or less concave.

The plastron remains inadequately known. The best fragments belong to P26238 (pl. 28). They consist of a medial half of the left hyoplastron, the medial end of the right hypoplastron and the greater portion of the left xiphiplastron. These fragments show a typically toxochelyid condition, but do not permit a more detailed comparison with the plastra of other genera. All three fragments show pronounced keel knobs on their ventral surfaces, much as in *Ctenochelys*, and the xiphiplastron resembles in outline that of *C. acris*.

***Prionochelys matutina* sp. nov.**

Type.—C.N.H.M. P27561, partial carapace and plastron, elements of pelvis.

Horizon and locality.—Mooreville Chalk, Selma Formation, Late Cretaceous. Moore Brothers farm, Harrell Station area, Dallas County, Alabama.

Referred specimens.—Eutaw area, Greene County, Alabama: C.N.H.M. PR31, crushed peripherals.

Harrell Station area, Dallas County, Alabama: C.N.H.M. P27479, large peripheral; C.N.H.M. PR222, nuchal and first peripheral of large individual.

West Greene area, Greene County, Alabama: C.N.H.M. PR185, peripherals, pygal, neural, and costal of juvenile specimen.

Diagnosis.—Species closely related to *P. nauta*, but with much less acute keel profile. Ridge line of neural 2 only half the distance between anterior and posterior sutures. Neural 8 not reduced in length as in *P. nauta*. No anal elevation. Marginal edge of pygal sharp. Xiphiplastron widest in front of keel knob.

Description.—The material on which this species is based consists of the remains of very small, medium-sized, and large individuals. PR222, consisting of the nuchal and left first peripheral only, indicates a turtle of about the same size as *P. nauta*. The more adequate specimens are thus considered subadult (P27561, type specimen) and juvenile (PR185). In view of the fact that a number of differences, apparently brought about by differential growth rates of

the various carapacial elements, were noted in two large specimens, of unequal size, of *P. nauta*, the morphology of these rather young individuals of *P. matutina* should be evaluated with care.

In comparing the type specimen of this species with the smaller individual of *P. nauta* (P26238), it may be noted that elements of the keel are about two-

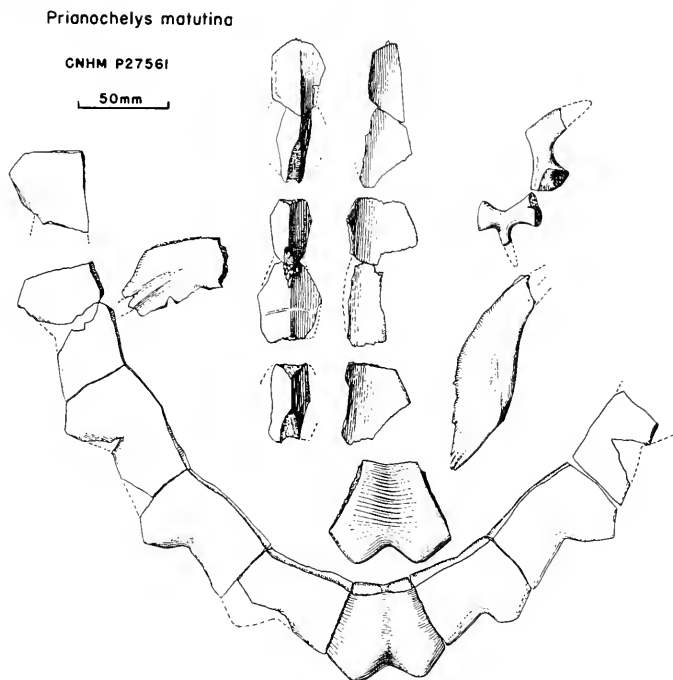


FIG. 118. Type specimen of *Prionochelys matutina* (C.N.H.M. P27561).

thirds the size of those of P26238, whereas the xiphiplastra of the two specimens are of nearly equal size (fig. 119). Since the neural series determines, to a great extent, the length of the carapace, I am inclined to consider the size relationship between the neurals (rather than that between the xiphiplastra) as an approximate indication of the over-all size category of the two specimens. The morphology of the neural keel in the type specimen of *P. matutina* may thus differ in detail from that of a fully grown individual, and adult specimens of both species might reveal a greater or lesser degree of similarity than do the specimens now at hand.

I do not believe, however, that the keel differentiation as seen in the type specimen of *P. matutina* merely represents an earlier ontogenetic stage in a developmental series ending with the condition observed in *P. nauta*. It is a

general rule, in turtles, that spines and ornamental processes on the shell are far more pronounced and acute in juveniles than in adults. A difference in this regard is seen even in the two unquestionably adult individuals of *P. nauta* (P26237 and P26238). The keel of *P. matutina* is blunt by comparison with the larger specimen of *P. nauta*, and its adult differentiation is likely to be less rather than more acute. In view of these considerations, I am inclined to regard the keel differentiation in *P. matutina*, even though materials of comparable size are not available, as notably more primitive than that of *P. nauta*.

The neural elements of P27561 (fig. 118) are basically similar in structure to those in *P. nauta*. The keel elevations are lower and less abrupt, and there are differences in proportion among the elements, as is readily seen in figure 114. Neural 2 has a much shorter, and neurals 5 and 8 a much longer, ridge line than their homologues in *P. nauta*. In the abdominal keel elevation, the epineural ossicle is a rather insignificant bone, to judge from the suture scars on neurals 5 and 6. The pygal plate is of ordinary shape, lacking a scar for an epithecal ossicle (fig. 118). It is, on the whole, convex both dorsally and ventrally, except for a shallow depression along the ventral mid-line. Its marginal border is sharp. A small sagittal process on the anterior face of the pygal indicates that the suprapygal tapered to a very narrow, rod-like plate posteriorly, and that the lateral fontanelles extended very close to the mid-line. Only the posterior peripherals are known in the type specimen. They form a deeply serrated margin as in *P. nauta*. The anterior suture of peripheral 11 is less oblique than in *P. nauta*, indicating that the carapace was more evenly pointed posteriorly. Very little is known of the costal plates. One posterior element, possibly the left eighth, is thin, distally barely covering the underlying rib.

The plastron is represented only by the left xiphiplastron. It is a sturdy bone with a strong keel knob on its ventral face near the lateral edge. The shape of this plate differs notably from that of the xiphiplastron in *P. nauta* (pl. 28). It is widest at mid-length and resembles in outline the xiphiplastron of *Ctenochelys tenuitesta*.

Both ischia and the left ilium are present in P27561 (fig. 118). The ilium shows typical toxochelyid shape but no specific peculiarities. The ischium is wider laterally than medially and possesses a spur that faces postero-laterad. This again appears to be typical for toxochelyid turtles in general, and side by side comparison with the ischia of *Toxochelys moorevillensis* (P27391) shows a remarkable degree of similarity in this element among otherwise very different animals.

A noteworthy specimen is the juvenile individual PR185. It consists of two lateral and the tenth and eleventh peripherals, the pygal, the ninth neural, and a small posterior costal. In linear measurement, it is less than half the size of P27561 (length of pygal along mid-line: P27561, 46 mm.; PR185, 20 mm.). The pygal, entirely uncrushed, is very thick for its size (maximal thickness 10 mm.) and strongly convex from side to side dorsally. The ventral face is also convex, except for a depression along the mid-line as in the type specimen.

On the anterior face, there is a relatively large area for the junction with the suprapygal.

Comparison with the eleventh peripheral of P27561 shows an interesting detail concerning the growth of this plate and that of the pygal. It may be noted in figure 120 that the anterior (oblique) suture face of the eleventh peripheral of P27561 does not form a straight contact line with the preceding peripheral; the marginal third of this line forms an angle of about 20° with the inner two-thirds. In PR185, this suture line is straight. Enlarging (photographically) PR185, so that its anterior suture face corresponds in length to the inner two-thirds of the suture in P27561 (fig. 120), brings the centers of ossification of the peripherals and pygals into congruence. This indicates that up to the two-thirds mark of the anterior suture in P27561 most of the growth in width of the peripheral took place medial to the center of ossification; then the direction of growth was reversed and the element grew marginally outside of the center of ossification. The pygal plate, as would be expected, underwent a similar two-phase growth, first forward, then marginal.

Prionochelys nouto

Prionochelys matutina

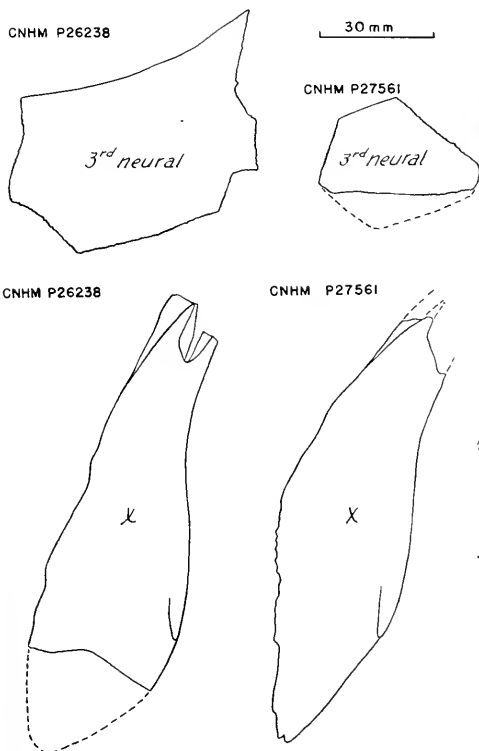


FIG. 119. Comparison of relative sizes of third neural plates and xiphoplastra in *Prionochelys nouto* and *P. matutina*.

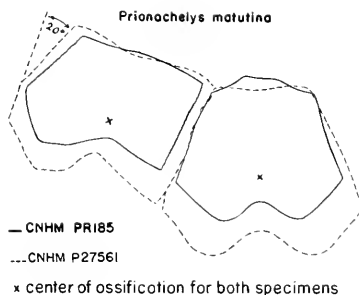


FIG. 120. Mode of ossification (growth) in pygal and eleventh peripheral plates of *Prionochelys matutina*, as suggested by two different ontogenetic stages.

The ninth neural shows two interesting features. Anteriorly, at this juvenile stage, the epithecal ossicle is small and has not yet formed a sutural contact with neural 9. This is in agreement with observations reported earlier (Zangerl, 1939) to the effect that epithecal ossifications are acquired relatively late in ontogeny, always after the anlage of the thecal plates. Judging from the suture scar on the eighth neural in P27561 (fig. 118), there is no doubt that the epineural made sutural contact with neural 9 in this older specimen, as shown in figure 114. On the posterior end of neural 9 of PR185, there is a long dorsal process that must have been locked into the anterior margin of the suprapygal as illustrated in figure 114.

The largest specimen (PR222) consists of the badly weathered nuchal fragment and the left first peripheral. These elements indicate great similarity to the corresponding plates of the largest specimens of *P. nauta*. The nuchal, however, is strongly arched from side to side near the mid-line and some distance back of the cervical edge.

***Prionochelys galeotergum* sp. nov.**

Type.—C.N.H.M. PR125, fragmentary carapace of subadult individual. Collected by Mr. G. F. Sternberg, 1931.

Horizon and locality.—Niobrara Formation, Late Cretaceous. Cove County, Kansas.

Diagnosis.—Most primitive member of the genus. Elevations of the neural keel formed by large epithecal ossicles only. Epithecals anchored in deep twin pits on neurals. Anal elevation present. Post-nuchal fontanelles in young individual. A knob near mid-line on dorsal face of nuchal plate, close to cervical edge. Marginal edge of pygal blunt.

Description.—The type is the only known specimen. It was purchased from Mr. G. F. Sternberg along with a number of other fragmentary but highly interesting turtle materials. The label indicates no specific locality.

All of the identifiable parts of this specimen are illustrated in figure 121. PR125 is about two-thirds the size of the type specimen of *P. matutina*; it is thus probably a rather young individual.

The shape and deep serration of the posterior peripherals are very similar to *P. matutina* and the neural keel shows the epithecal ossicles spaced three thecal neurals apart (fig. 114). The generic affiliation of this form is thus in no doubt. With regard to the differentiation of the neural keel, however, *P. galeotergum* is much more primitive than the other two species. As in *Ctenochelys*, the epithecal ossicles alone form the keel elevations (figs. 114 and 121). The epineural elements have a characteristic shape and are connected with the underlying neural plates by an unusual sutural contact. At the junction of neurals 2 and 3, there is a very deep sutural pit into which the anterior portion of the epineural was locked. A second and more shallow pit lies behind the first and is separated from it by a ridge. On the under side of the epineural, there is a

depression that fits over the ridge between the pits on the neural plates (fig. 121). In contrast to *P. matutina*, this form has an anal elevation, an epithecal ossicle overlying the junction of the suprapygal and the pygal plates (fig. 121). The pygal is thick and its marginal edge is blunt rather than sharp as in *P. matutina*. It is far narrower anteriorly than in the compared species (fig. 121).

The nuchal plate is incomplete, but shows a number of important features. Postero-laterally, the fragment shows a thin, natural edge indicating the presence of post-nuchal fontanelles. The anterior margin is moderately excavated. A small knob is located on the mid-line between the cervical edge and the anterior shield furrow of the first vertebral shield (fig. 121). The lateral extent of the nuchal shield cannot be determined satisfactorily. The dorsal face of the nuchal is gently arched from side to side.

The two anterior peripherals, numbers 3 right and 4 left (fig. 121), do not show distinct rib-pits and neither does the tenth. There is an abnormality in the posterior peripheral series on the right side. Instead of an eleventh peripheral,

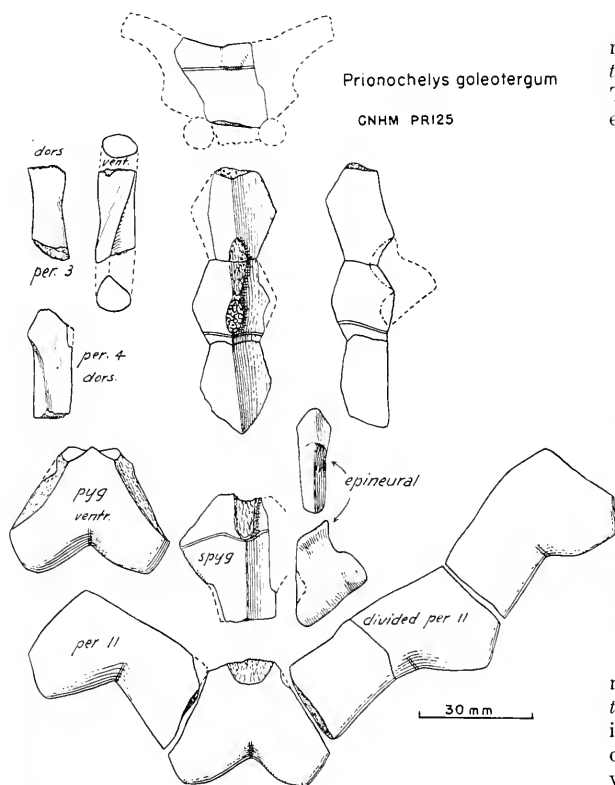


FIG. 121. Type specimen of *Prionochelys galeotergum* (C.N.H.M. PR125). The right eleventh peripheral is abnormally divided.



FIG. 122. Neural fragment of *Ctenochelys tenuitesta* (C.N.H.M. P27425) in lateral view (keel ridge on left side), showing severe parasitic lesions.

there are two plates, neither equivalent in size and shape to the eleventh element on the left side.

In addition to the bones described, there are fragments belonging to the costal plates, peripherals, and hyo- or hypoplastron.

Forms Questionably Referred to the Toxochelyidae

A number of forms that have been referred to the Toxochelyidae can not readily be identified as belonging to any of the three subfamilies distinguished above, and there is no convincing reason why any of these species should be included in this family. It may be, of course, that the Toxochelyidae had a much wider distribution and that forms from other continents may represent additional subfamily patterns. On the basis of the present record this is not a likely probability.

Cynocercus incisivus Cope

Cynocercus incisivus Cope, Proc. Amer. Phil. Soc., **12**, p. 308, 1872; Proc. Acad. Nat. Sci. Phila., p. 129, 1872; Fifth Ann. Rept. U. S. Geol. Surv. Montana, . . . p. 335, 1871 (1872); Rept. U. S. Geol. Surv. Terr., **2**, pp. 96, 260, pl. 8, figs. 3-5, 1875; Williston, Univ. Kansas Geol. Surv., **4**, p. 368, fig. 6, 1898; Hay, Field Columb. Mus., Zool., **1**, p. 106, 1896; U. S. Geol. Surv. Bull., **179**, p. 442, 1902; Carnegie Inst. Wash. Publ., **75**, p. 180, 1908.

This species is based on a few caudal vertebrae and a metapodial bone, probably from the Niobrara Chalk of Kansas. The specimens are described and illustrated by Cope and Williston as cited above. The vertebrae differ in a number of respects from those few caudal vertebrae known in *Toxochelys* and *Ctenochelys*, even though elements of probably the same general region of the tail are available for comparison. It is possible that *Cynocercus* is not a toxochelyid, but the matter cannot be decided at present.

Toxochelys gigantea Oertel

Toxochelys gigantea Oertel, Jahresber. Niedersächs. Geol. Ver. Hannover, **7**, pp. 91-106, 1 fig., 1914.

Under the above name Oertel described an isolated, very large skull (± 250 mm. sagittal length) of a chelonian from the lower Aptian of Karstendamm, near Hannover, Germany. The posterior half of the skull roof is missing and the anterior part is crushed to the left side. The palatal aspect of the skull is fairly complete. Of particular interest is the area of the vomer and the palatines. The situation is essentially the same as in *Ctenochelys* in the sense that the roof of the mouth cavity exhibits a condition intermediate between a primary and a secondary palate. The vomer and the lateral portions of the palatines are unusually rugose and a partial undershelfing of the choanal passages seems to have taken place. In detail this area differs, however, considerably from that of *Ctenochelys*.

In attempting to decide whether or not this species represents a toxochelyid, it should be remembered that the toxochelyid skull is in many ways similar to that of the Cheloniidae and differs from it primarily in the region of the palate. The secondary cheloniid palate is unquestionably derived from a primary palate and intermediate conditions are thus to be expected in the Cheloniidae as much as in the Toxochelyidae. In my opinion the skull described by Oertel belonged to a cheloniid rather than a toxochelyid turtle.

Sinemys lens Wiman

Sinemys lens Wiman, Palaeontogr. Sinica, ser. C, 6, (3), p. 7, pl. 1, figs. 1-4, pl. 2, figs. 1-4, pl. 3, figs. 1-5, 1930; Nopcsa, Centralbl. Min. Geol. Pal., (B), p. 510, 1930.

The material on which Wiman's species is based consists of seven specimens of partial shells of different size. Nopcsa (1930) reviewed Wiman's description and illustrations and decided that *Sinemys* is a "definitely primitive cheloniid belonging to the Lytolominae," the exponent representative of which group Nopcsa considered to be *Osteopygis*; he actually compared *Sinemys* with this genus. It seems certain that Nopcsa's familiarity with *Osteopygis* was from the literature only; I doubt that he would have been so definite in his conclusion had he actually seen specimens of *Osteopygis*.

Sinemys differs from all unquestionable toxochelyid turtles in so many respects that its inclusion in the family would constitute an arbitrary procedure at the present state of our knowledge of the group. The carapace of *Sinemys*, a small turtle (approximate carapace length of largest specimen—an adult, judging by the proportions of the vertebral shields—is 190 mm.), differs from Toxochelyidae in the suprapygial area, in the mode in which the peripheral plates are sutured to the costals, and in the number of neural plates. But the most remarkable feature is the lack of lateral fontanelles even in the smallest individual (carapace length about 70 mm.). In all toxochelyids the juveniles have larger fontanelles than the adults.

The plastron is preserved only in two very small individuals (Wiman, 1930, pl. 1, figs. 1, *b*, and 2, *a*). Again, it is most peculiar, since hyo-, hypo-, and xiphiplastra are sutured along the mid-line, leaving a large umbilical fontanelle and apparently no lateral fontanelles (loc. cit., pl. 1, fig. 2, *a*, left side of picture). The axillary and inguinal notches are not as deeply excavated as in toxochelyid turtles, the axillo-inguinal distance being 80 per cent of half the width of the plastron, whereas in the most advanced toxochelyid forms it is only 60 per cent or less and in the primitive genera around 35 per cent. The posterior lobe of the plastron of *Sinemys* is much longer and narrower than in any toxochelyid.

Sinemys is stated to be of Early Cretaceous age; it is thus much older than the toxochelyid turtles discussed above.

Sinemys could well be a turtle remotely related to the Cheloniidae and the Toxochelyidae. There is no reason to deny, on the basis of present knowledge, a likewise remote relationship to the Chelydridae and the Dermatemydidae.

It has, to my knowledge, not been pointed out that *Sinemys* might be an advanced plesiochelyid. A comparison of the plastron with that of *Plesiochelys etalloni*, and the carapace (with its short and wide first vertebral shield, and with a similar suture pattern between peripherals and costals) with that of a number of species of *Plesiochelys* is, I believe, rather suggestive. The relatively narrow vertebral shields and the greater slenderness of the posterior lobe of the plastron in *Sinemys* should not be regarded as a serious obstacle to this interpretation, since there is a tendency in both these directions among various species of *Plesiochelys*.

THE PALEOECOLOGY OF THE TOXOCHELYIDAE

Horizontal and Vertical Distribution

The geographical distribution of the toxochelyid turtles is, so far as is definitely known, restricted to the coastal waters in the southern half of the East Block of the Cretaceous North American Continent (Eastland; see W. A. VerWiebe, 1933). On the west side of this land mass they inhabited the relatively shallow, intracontinental Niobrara-Pierre Sea; in the south they populated the Gulf shores from eastern Texas to Alabama and were apparently abundant along the Cretaceous coast of New Jersey. It would seem reasonable to assume that the shores between the coastal areas mentioned were likewise inhabited by these turtles. The absence of records is due to a number of circumstances, such as unfavorable physiographic conditions for fossil collecting, for instance in Georgia; lack of determined collecting efforts in formations with meager fossil occurrence; and application of soil conservation programs that prevent large scale erosion in potentially fossiliferous areas.

While the distribution of these turtles, at the family level, presents a fairly clear-cut picture, it must be kept in mind that they were seafaring animals and may well have ranged farther south along the Cretaceous shores of Central America. It is, of course, possible that the toxochelyid turtles occurred in Europe, but the one record, a skull described as *Toxochelys gigantea* by Oertel (1914), is in all probability a cheloniid (see p. 260).

On the generic level it is worth noting that *Toxochelys*, probably the most common type of turtle in the coastal waters at the time, is represented in every formation from which toxochelyid turtles have been recorded. There is no evidence that *Osteopygis*, or even a closely related genus, occurs anywhere but on the east coast. *Thinochelys* and *Porthochelys* are rare in the formations in which they occur and may be found elsewhere in the future. *Lophochelys*, *Ctenochelys*, and *Prionochelys* were well represented along the Gulf coast and in the Niobrara waters, but none of these genera ranged as far as the Atlantic coast.

Of the three subfamilies distinguished above, the Toxochelyinae extend throughout the range of the family as a whole, but the Osteopyginae and Lophochelyinae occupy mutually exclusive geographic areas.

Little need be said about the species distribution, since the record is far too incomplete to merit discussion. In the Mooreville Chalk of Alabama there is no doubt but that all of the common species occur all along the strike of the outcrop area of the marls from the western border of the state to the region of Montgomery.

Most of the toxochelyid turtles are of Senonian age. If all of the labels on the Greensand materials of New Jersey are to be trusted, *Osteopygis* may extend well into the early Tertiary (Eocene). *Toxochelys* ranges vertically from Coniacian to early Maestrichtian time, the lophochelyine genera from Coniacian to late Campanian, and *Osteopygis* probably from early Maestrichtian time on, possibly into the Tertiary.

Very little is known as to the vertical range of species. In the Mooreville Chalk of Alabama there is no evidence to the effect that various species are stratigraphically restricted. All common species appear to occur throughout the Mooreville Chalk profile.

Habitat

There is no question but that all of the formations in which toxochelyid turtles occur are either near-shore deposits, or beds laid down in shallow inland waters (Niobrara-Pierre Sea). However, these may not have been the habitat of all species; the question of habitat and burial ground should be discussed in somewhat greater detail in the case of the Mooreville Chalk, where systematic, unbiased collections of all vertebrate remains, regardless of how fragmentary, were made over a period of years.

The relative frequency of occurrence of the different species is as follows: *Toxochelys moorevillensis*, 52 (5 good shells); *Thinochelys lapisossea*, 4 (1 good shell); *Lophochelys venatrix*, 4 (fragmentary); *Ctenochelys tenuitesta*, 38 (fragmentary); *C. acris*, 13 (fragmentary); *Prionochelys matutina*, 5 (fragmentary).

The two most abundant species are *Toxochelys moorevillensis* and *Ctenochelys tenuitesta*; the remaining species are rare by comparison. Since the sediments in which these forms are buried are not in the immediate vicinity of the shore line, and since the skeletons are not found in abundance in any one horizon and area, there is no apparent correlation between the occurrence figures and egg-laying behavior, that is, seasonal concentration of individuals near shore. The fragmentary nature of most of the specimens is not solely due to the erosion prior to collection of the specimens (see below). If that were the case one should expect a much higher percentage of nearly complete skeletons. The burial position of the bones in such specimens as were found in place shows clearly that the skeletons were severely macerated and often became scattered before burial. Entirely articulated shells were never encountered. It would thus seem that the death rate, from whatever causes, was fairly evenly distributed in time and over a large area. Under these circumstances the figures of relative frequency of occurrence may indicate that the common species lived in the waters that produced their burial ground (that is, the waters directly above).

In the case of the relatively rare species it is probable that their habitats were more or less distant from the burial ground. *Thinochelys*, for example, is a large, heavy-shelled form, and, by comparison, not as well adapted for a marine existence as *Ctenochelys tenuitesta*. It is conceivable that *Thinochelys lapissosca* lived in coastal swamps and large inlets and ventured away from the shore only occasionally. *Ctenochelys acris* may have frequented the region of the burial ground, but was essentially a pelagic form; the same, possibly, might be true of *Prionochelys matutina*.

Food

The differentiation of the jaws is not a good indicator of food habits in turtles. A secondary palate, for example, is not necessarily indicative of a durophagous diet, for it occurs also in species that feed exclusively on plant materials (for example, *Chelonia mydas*). On the other hand, a jaw apparatus of the type of Recent snapping turtles such as *Chelydra serpentina* is likewise unreliable as an indicator of exclusive fish or even exclusive animal diet. *Chelydra* itself consumes large quantities of vegetable materials (Lagler, 1943). Invertebrates occur in the burial ground, but they are not particularly numerous. Remains of a variety of fishes, including elasmobranchs, are relatively common and so are poorly preserved plant remains. The burial ground itself thus contains a considerable variety of potential sources of food, none of which is so abundant as to dominate the specific character of the biotope.

There is, unfortunately, no acceptable evidence suggestive of the probable food habits of the toxochelyid turtles, a matter of potential interest, in view of the fact that the transition from a primary palate to a secondary palate is realized within the group.

Locomotion

Functional analysis of the girdle and limb skeleton of *Toxochelys* (see p. 163) would seem to indicate a transitional type between the typical mode of locomotion of fresh-water turtles and that of true sea turtles. There is, indeed, good reason to believe that *Toxochelys* was capable of fast, short-distance propulsion in the general manner of trionychid turtles, and of cruising in the fashion of cheloniid turtles, but it may be assumed that neither type of locomotion was as efficient as it is in the compared groups. Ecologically, the toxochelyid type of locomotion suggests a greater home range of the individuals than has been determined for a number of Recent fresh-water forms (Cagle, 1944). In the latter the home range appears to be remarkably limited.

Parasitic Infestation

Parasitic lesions in the shells of toxochelyid turtles are very common; nearly every specimen shows at least minor parasitic erosions. As a rule, these are shallow pits of varying size and usually more or less circular outline. In

some cases these lesions perforate the shell entirely. The most severely infested specimens belong to *Ctenochelys tenuitesta*, where the keel-forming neurals, in particular, but also the peripherals often contain numerous, large erosion cavities (fig. 122). As a rule the lesions are larger on the outside of the shell, or, on the peripherals, on the side on which the infestation began. In cases of perforation, the inner opening is usually smaller in diameter than the outer opening. In other cases both outer and inner openings are small but there is an enlarged cavity in between. There is, at the moment, no way of determining whether these different lesions were caused by the activity of one or of several kinds of parasites.

In microscopic section the parasitic lesions show dense bone of varying thickness surrounding the cavities. Apparently there is an increased deposition of bone in the vicinity of many erosions, often producing notable, local thickening of the plates above and below the cavities.

Burial Conditions

Entirely articulated shells have not been found in the Mooreville Chalk. A number of specimens of *Toxochelys moorevillensis* and one specimen of *Thinochelys lapisossea* comprise so large a portion of the shell and even some vertebrae, girdle, and limb bones that we may assume that the carcasses were left undisturbed; but the bones were not, or were only partially articulated. It seems certain in all cases that the carcasses became severely macerated prior to being covered by sediment. Most of them, however, fell victim to scavengers and the skeletons became scattered. By far the greatest number of specimens consist of only a small portion of the shell; surface erosion prior to the collection of the specimens, no doubt, rendered them even less complete than they were, but I do not believe that this is the primary cause for the great abundance of partial specimens. In a few instances we have direct evidence in field observation that carcasses were scattered before burial. Specimens containing bones of the skull or mandible are exceedingly rare, which is the general rule in fossil turtles.

The burial conditions in the Niobrara Chalk may differ from those in the Mooreville Chalk, to judge from the abundance of fine skulls and the rarity of shells in the collections. In the Greensand of New Jersey the general situation is profoundly different. The shells are, probably for the most part, preserved in articulation.¹

THE RELATIONSHIP OF THE TOXOCHELYIDAE TO OTHER FAMILIES OF TURTLES

In the following an attempt will be made to outline the basic structural plan of the Toxochelyidae in the light of the basic patterns of families such as the Cheloniidae (*sens. lat.*) and the Thalassemyidae, in order to determine, more

¹ Two essentially complete shells of different turtles, not belonging to this family, were recently collected with proper care and may be cited as evidence.

clearly than has hitherto been possible, the typical organization of the three groups.

Comparison of Thalassemyid with Toxochelyid Pattern

The Thalassemyidae are a group of late Jurassic, marine turtles, restricted geographically (so far as is known) to Europe. The genera *Acichelys*, *Thalassemys*, *Idiuchelys*, *Chelonides*, *Hydropelta*, and *Pelobatochelys* represent a group of forms that undoubtedly are closely related to each other and to the Plesiochelyidae, as I had an opportunity to learn by examination of the famous Solothurn materials and those from Cerin preserved in the Museum of Lyon, France. The genera mentioned above are generally agreed upon as forming the family Thalassemyidae, but some authors, as, for example, Lydekker (1889), include, probably for convenience, the genus *Tropidemys*. This form is difficult to assign to any presently recognized family, but it is almost certainly not a thalassemyid.

The above statement to the effect that the Thalassemyidae are closely related to the Plesiochelyidae is based on personal study of the species of both *Plesiochelys* and *Thalassemys* from Solothurn.¹

As far as the Solothurn species are concerned, the genera *Plesiochelys* and *Thalassemys* can only be distinguished by characters of a mostly quantitative nature, as follows:

<i>Plesiochelys</i>	<i>Thalassemys</i>
No costo-peripheral fontanelles	Costo-peripheral fontanelles
Carapace highly arched	Carapace fairly flat
Anterior lobe of plastron normal	Anterior lobe of plastron lacking epiplastra and possibly entoplastron
Medial suture between xiphiplastra	Xiphiplastra free medially (except in Neuenburg specimen)
Plastron suturally attached to carapace	Plastron attached to carapace by dermal connective tissue
Plastron without lateral fontanelles	Plastron in some specimens with lateral fontanelles
Vertebral shields relatively wider than in <i>Thalassemys</i>	

Needless to say, differences of this kind can hardly be considered to justify family distinction, but it must be pointed out that the species of *Thalassemys* from the Solothurn quarries are among the most primitive of all thalassemyids. The differences stated are nearly all correlated with increased aquatic specialization in *Thalassemys*. There is little doubt as to the origin of the Thalassemyidae from the Plesiochelyidae, but the details of this relationship appear to be complicated and should be considered in future revisions of the pertaining groups.

For the comparison below it may be permissible to regard thalassemyid turtles as a closely related group of marine forms of different degrees of aquatic

¹ Since Rüttimeyer (1873) described the materials from Solothurn, much additional material has accumulated, with the result that some of the problems that confronted Rüttimeyer are now within sight of solution.

specialization. The Thalassemyidae and the Toxochelyidae thus differ in the following features of their organizations:

<i>Thalassemyidae</i>	<i>Toxochelyidae</i>
Carapace	
Vertebral shields always much wider than pleural shields	Vertebral shields always much narrower than pleural shields
Neural plates tend to be suppressed	Neural series always normal
Usually one suprapygal	Two suprapygals
Plastron	
Distance between axillary and inguinal notches 90 per cent or more of half the width of the plastron	Distance between axillary and inguinal notches 60 per cent or less of half the width of the plastron

The dimensional difference mentioned above for the plastron determines the basic character of the ventral armor and is not affected by extreme aquatic specialization in either family. Besides the differences in the shells of the two families of turtles, there are important differences in the forelimb skeleton. *Idiochelys* has the typical forelimb of a fresh-water turtle, whereas *Toxochelys* possesses a flipper of essentially cheloniid structure and probable function.

Comparison of Cheloniid with Toxochelyid Pattern

Turtles of definitely cheloniid affinities are known from late Cretaceous time to the present. The Cretaceous forms are, on the whole, more highly specialized than the Recent representatives and some of those from Eocene deposits. Among the latter some are more primitive, others more specialized than the living species. The present evolutionary picture of this family is thus not one of gradual increase in aquatic specialization from an original generalized group; instead we seem to know primarily (but not exclusively) the advanced species of branches that appear to have developed from generalized, central stock repeatedly since Mid-Cretaceous time.

There are, beyond doubt, many similarities between the cheloniid turtles (particularly *Lepidochelys*) and the Toxochelyidae, and the two groups are very probably derivatives of generalized chelydrid stock. The morphology of the Cretaceous genus *Catapleura*, as well as the living genus *Lepidochelys* is nearly intermediate between the cheloniid and toxochelyid organizations; the trend of specialization of the plastra of both these genera is, however, cheloniid, rather than toxochelyid.

In view of this rather close relationship between the Cheloniidae and the Toxochelyidae, generalized species may be difficult to assign. In terms of trends of specialization, however, the two families diverge markedly. The most striking difference lies in the shape of the plastron, which in Toxochelyidae remains essentially cruciform, with a short axillo-inguinal distance and a relatively long hyo-hypoplastral contact suture. In the cheloniid plastron the axillo-inguinal distance increases from primitive to advanced genera and the hyo-hypoplastral

suture becomes progressively shorter (fig. 123). The epiplastra are always very small in Toxochelyidae, always well developed in Cheloniidae.

The carapace of all cheloniid turtles is oval to elongated-cordiform. In Toxochelyidae it is circular to oval, or broadly cordiform. Long and narrow shells are not known. The carapace of all Toxochelyidae is fringed by well-

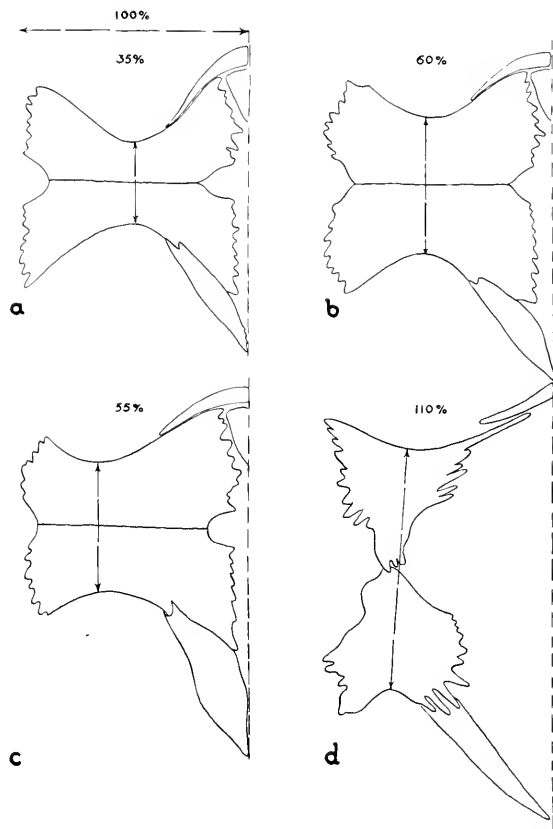


FIG. 123. Comparison of plastral differentiation in Toxochelyidae and Cheloniidae. (a), primitive toxochelyid; (b), advanced toxochelyid; (c), primitive cheloniid; (d), advanced cheloniid. Figures diagrammatic.

developed peripherals. In the Cheloniidae there is a trend toward reduction of the peripherals to narrow bars. The neural series of the toxochelyid carapace consists of 8-10 elements, either unkeeled or keeled; if keeled, it is serrated in side view and may or may not have epithecal ossicles associated with the keel elevations. Among the Cheloniidae keeled forms are exceptional (for example, in

Allopleuron and *Peritresius*) and if present, the keels are not serrated in side view in such a way as to form keel elevations underneath the apices of the vertebral shields (except in juvenile individuals of *Lepidochelys*). There appears to be a trend, furthermore, toward fragmentation of the neural plates, so that their number is notably increased (*Lepidochelys*, *Procolpocheilus*).

With the exception of *Osteopygis*, the toxochelyid skull has a technically primary palate; that of the Cheloniidae, so far as definitely known, has a secondary palate (but see remarks concerning "*Toxochelys*" *gigantea*, p. 260). In the toxochelyid skull small nasal bones are present, in the Cheloniidae these are reduced.

At the present state of knowledge, the Toxochelyidae and Cheloniidae differ with regard to the normal pattern of cervical central articulation. The normal formula in the Toxochelyidae corresponds with that of the Recent Chelydridae (see p. 155). In the cheloniid turtles the most common pattern shows plane joint surfaces between centra 6 and 7 (Williams, 1950).

The above discussion thus leads to the conclusion that the Toxochelyidae and the Cheloniidae are marine families of similar origin that existed together during Cretaceous time. The direction of specialization in the marine habitat differs, however, considerably in the two families.

MORPHOLOGICAL AND PHYLOGENETIC RELATIONSHIPS AMONG THE TOXOCHELYIDAE

If the over-all organization of the turtles of the family Toxochelyidae is considered, it may be noted that the genera differ from each other in features that are, in one way or another, connected with aquatic specialization. The thickness of the shell, the circular or oblong outline of the carapace, fontanellization, the presence of a mid-dorsal carina, and the development of a secondary palate are all features of aquatic adaptation. None of the genera known at present are specialized in all of these features but, as expected, they combine primitive with advanced characters.

If we combine the generalized features of all toxochelyid turtles we arrive at an unkeeled form with heavy shell plates and oval carapace outline and with all carapace plates joined by sutures as in some specimens of *Osteopygis*. The plastron would have small lateral and umbilical fontanelles and be excavated at the axillary and inguinal notches to the extent observed in *Porthochelys*; its lateral attachment to the peripherals, however, would be as in *Osteopygis*; the skull would have a smooth, primary palate as in *Toxochelys*. A comparison of the genera with this morphotypic form is shown in figure 124.

There is no evidence in this group that the trends of specialization of the features mentioned were changed or reversed. The outline of the carapace of *Toxochelys*, for example, is nearly circular in the relatively primitive *T. moore-*

rillensis as well as in the much more specialized *T. latiremis* and *T. atlantica*. Figure 124 shows that only two genera (*Lophochelys* and *Ctenochelys*) are similarly specialized in such a way that the more advanced *Ctenochelys* could have been derived from the more generalized condition, as in *Lophochelys*.

A faint trend toward keeled neurals is seen in young specimens of *Toxochelys*, where they are very gently arched from side to side. It is possible that the keeled genera originated from early *Toxochelys* stock. Since all of the genera, with the exception of *Osteopygis*, occur in the same deposits, namely, the Mooreville Chalk of Alabama and the Niobrara Chalk of Kansas, and very probably at the same stratigraphic levels within these formations, we have to assume that their differentiation lies farther back in time.

The relationship between the species, occurring at different stratigraphic levels, is of notable interest, since it is different from what might have been expected. The stratigraphically oldest species of *Toxochelys* is *T. latiremis* from the Niobrara, yet it is as highly specialized or more so than the youngest member of the genus, *T. atlantica* from the Upper Greensand of New Jersey. The better known species of *Toxochelys*, arranged according to their stratigraphic age and their relative degrees of specialization, produce the following picture:

Order of decrease in stratigraphic age: *T. latiremis*, *T. moorevillensis*, *T. barberi*, *T. atlantica*.

Order of increase in specialization: *T. moorevillensis*, *T. barberi*, *T. atlantica*, *T. latiremis*.

T. moorevillensis, *T. barberi*, and *T. atlantica* are forms that occur along the open waters of the Gulf and Atlantic coasts, whereas *T. latiremis* lived in a semi-isolated inland basin. We may thus assume that *T. latiremis* underwent specialization earlier and at a faster rate than its relatives along the Gulf coast, a phenomenon possibly correlated with limited population size in the Niobrara Sea.

The three species of *Prionochelys*, *galeotergum* (Niobrara), *matutina* (Mooreville Chalk), and *nauta* (Marlbrook Marl), show a different picture. In this series, the stratigraphically oldest species is also the most primitive, while the youngest is the most advanced form. If *P. matutina* and *P. nauta* are compared, there can be little doubt that they are very closely related; in every feature *P. matutina* shows a somewhat more primitive condition than does *P. nauta*. The situation strongly suggests a direct ancestor-descendant relationship between these two species. The Niobrara form, *P. galeotergum*, although more primitive than *P. matutina*, differs from the latter in particular details of keel specialization (see fig. 114) and represents a different line within the genus.

The evidence in the cases of *Toxochelys* and *Prionochelys* strongly suggests a progressive isolation of the Niobrara Sea from the open Gulf waters, resulting in the evolution of endemic species in the inland sea. If we consider, along with the faunal picture of the Niobrara Sea, that of the later Pierre Sea, we may note that *Toxochelys browni* can readily be interpreted as a direct descendant of *T. latiremis*; if so, it appears to have increased in size considerably. Further-

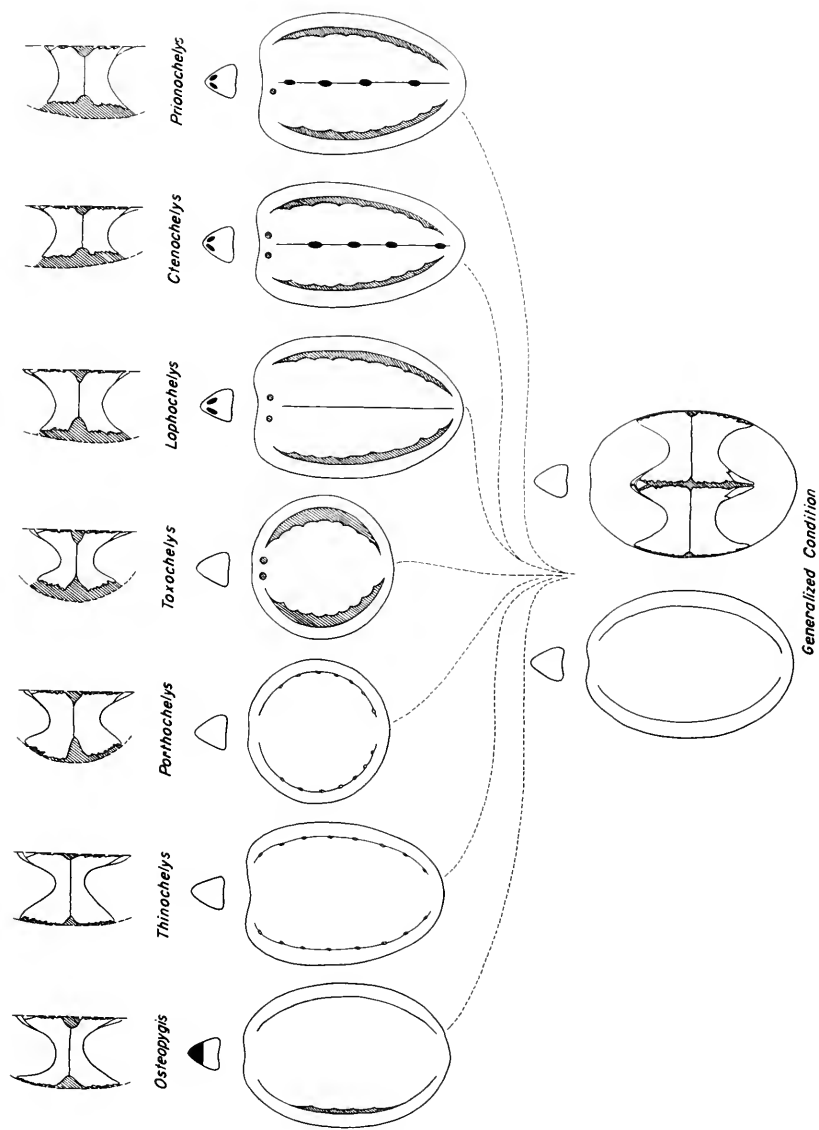


FIG. 124. Diagrammatic representation of the state of specialization in the seven genera of toxochelyid turtles and the morphological relationship of these forms to the morphotypic condition of the family.

more, *T. browni*, represented in the record by a fair number of specimens (skulls), appears to be the only toxochelyid turtle in the Pierre deposits; *Porthochelys*, *Lophochelys*, *Ctenochelys*, and *Prionochelys* seem to have become extinct in this inland sea. This may constitute an interesting parallel to the situation in the protostegid turtles (Part III, this volume), where there is likewise a reduction in the number of species to one, and an increase in the size of the surviving form (*Archelon ischyros*).

SUMMARY AND CONCLUSIONS

1. The present account represents a monographic study of the family Toxochelyidae, including a restudy of nearly all specimens of toxochelyid turtles known.

2. Since the last revision of the family a significant amount of new material has accumulated, primarily from the Mooreville Chalk of Alabama. All of the new materials are described.

3. The comparative osteology of the toxochelyid skeleton in general could be worked out satisfactorily, save for minor details. The skull and the cervical portion of the vertebral column are known in considerable detail. Small nasal bones are definitely present in *Toxochelys* and *Porthochelys*. The normal pattern of cervical central articulation is identical with that most commonly observed in Chelydridae.

4. A functional analysis of the type of locomotion in *Toxochelys* compared to that of fresh-water turtles (such as Chelydridae and Trionychidae) and sea turtles (Cheloniidae, Protostegidae, and Dermochelyidae) led to the conclusion that *Toxochelys* was capable of both types of propulsion, namely, of fast, short-distance locomotion by means of rapid paddling with the hind limbs, and of cruising by slow, simultaneous, vertical strokes of the forelimbs. The latter are interpreted as flippers, but appear to have been somewhat less specialized than in Recent cheloniids.

5. As here understood, the family Toxochelyidae contains three subfamilies with the following genera:

- A. The Toxochelyinae include the forms without a mid-dorsal carina on the carapace, and with a smooth primary palate: *Toxochelys*, *Thinochelys* gen. nov., and *Porthochelys*.
- B. The Osteopyginae include the forms with uncarinated shells, but with extreme secondary palates: *Osteopygis* and ?*Rhetecheles*.
- C. The Lophochelyinae include the forms with carinated shells, and with palates having partially undershelled choanal passages: *Lophochelys* gen. nov., *Ctenochelys* gen. nov., and *Prionochelys* gen. nov.

6. *Lytoloma angusta* Cope, *L. jeansi* Cope and *Chelone sopita* Leidy are considered to be nomina vana.

7. *Phyllemys* is synonymous with *Toxochelys*. *Catapleura* is thought to be a primitive cheloniid. *Sinemys*, regarded by Nopcsa as a relative of *Osteopygis*, is not a toxochelyid, but might be an advanced plesiochelyid turtle. *Cynocercus* is a very doubtful toxochelyid.

8. *Toxochelys brachyrhina* Case is interpreted as a badly flattened skull and *T. serrifer* Cope (non Case) as a nearly uncrushed partial skull of *Toxochelys latiremis*. *Toxochelys gigantea* Oertel is probably a cheloniid turtle.

9. The shell of *Lytoloma wielandi* Hay was recognized as *Toxochelys atlantica* sp. nov. The skull and mandible belong to *Ostocopygis*.

10. *Porthochelys browni* Hay is a species of *Toxochelys*.

11. The eight species of *Ostocopygis* recognized by Hay from the Greensand deposits of New Jersey are interpreted as belonging to one species.

12. *Toxochelys serrifer* Case (non Cope), *T. bauri* Wieland, and *T. elkader* Hay are tentatively regarded as synonymous with *T. stenopora* Hay; these are carinated forms belonging to the genus *Ctenochelys*. *Toxochelys procar* Hay is likewise a member of the genus *Ctenochelys*.

13. The geographical distribution of the toxochelyid turtles follows the shores of the southern half of the East Block of the Cretaceous North American Continent. In vertical direction the family ranges from Coniacian time to the close of the Cretaceous and, possibly, into the early Tertiary.

14. There is evidence (circumstantial) that the different species of toxochelyid turtles buried in the same formation occupied different habitats, some possibly the region that produced the burial ground.

15. There is no satisfactory evidence as to the probable food habits of toxochelyid turtles.

16. A possible ecological effect of the mode of locomotion of *Toxochelys* (see point 4) may have been the widening of the home range of the individuals.

17. The shells of most adult specimens of toxochelyid turtles show more or less severe parasitic lesions; there are no clues to the nature of the parasite.

18. The families Toxochelyidae and Thalassemyidae are not closely related; the two groups differ in the basic features of their organization. The families Toxochelyidae and Cheloniidae, on the other hand, are rather closely allied.

19. All of the genera (except *Osteopygis*) of the Toxochelyidae are co-existent in the Mooreville Chalk of Alabama and the Niobrara Chalk of Kansas. The morphological relationships between the genera are illustrated in figure 124, along with the morphotypic condition of the skeleton of the group as a whole.

20. The relationships between the species show a notable endemic differentiation of the Niobrara species, indicative of a progressive isolation of the Niobrara Sea from the open waters of the Gulf. In the Pierre Sea the toxochelyid fauna appears to be reduced to one species (*Toxochelys browni*) of large size—a

possible parallel to the reduction in the number of species and increase in size of the survivor among the Protostegidae (*Protostega*-*Archelon*).

21. *Prionochelys nauta* can be interpreted as a direct descendant of *P. matutina*.

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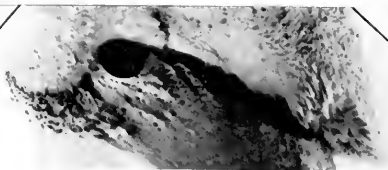
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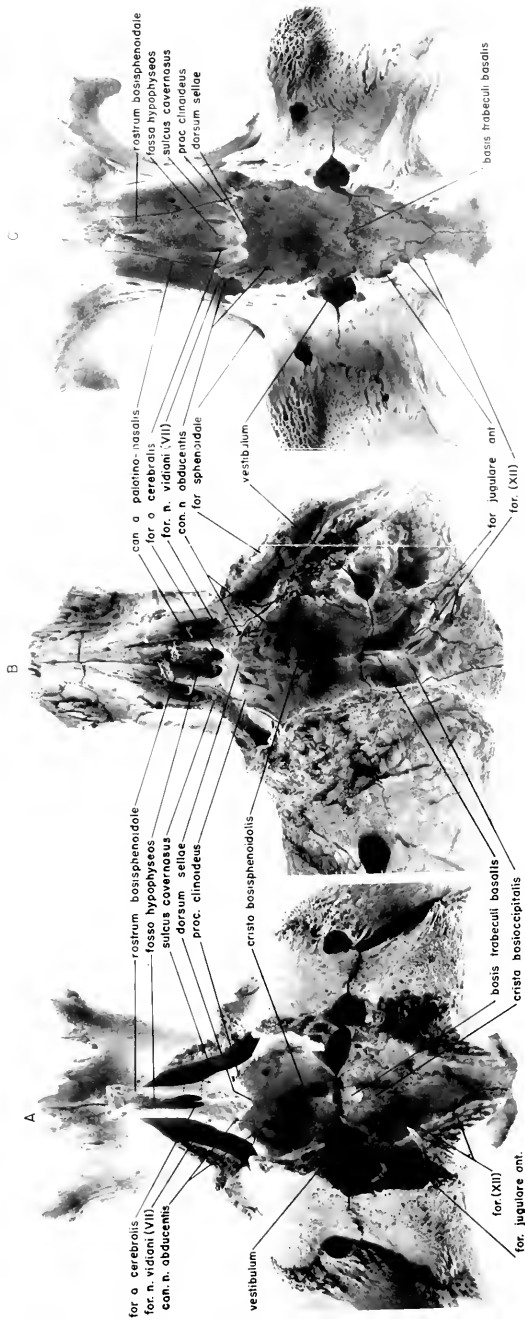
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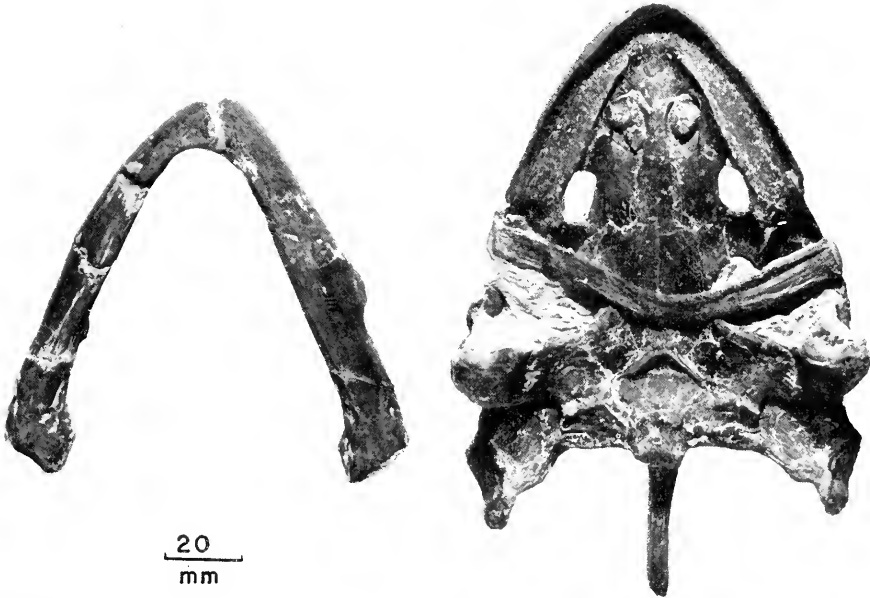
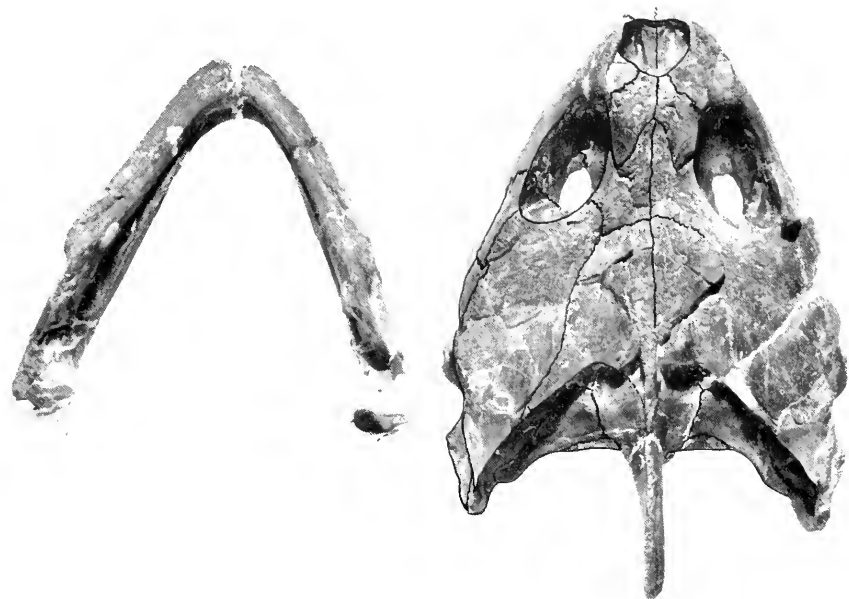


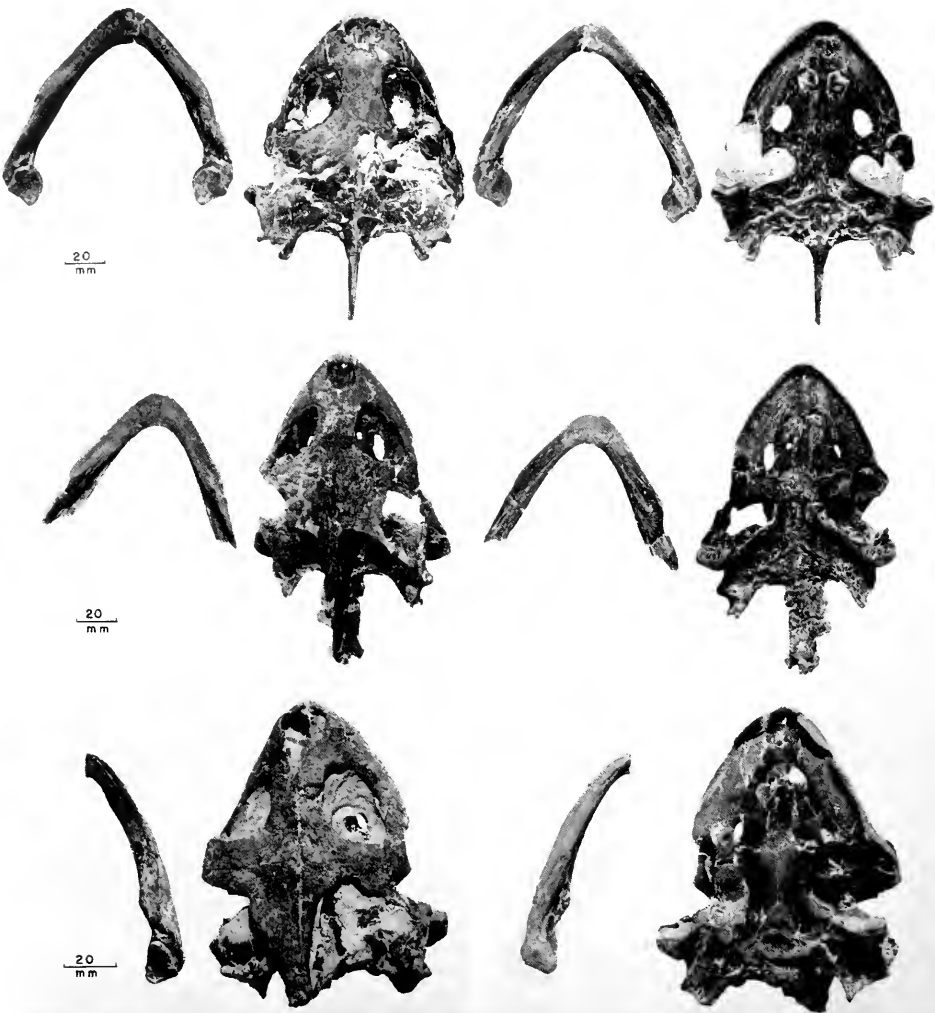
Comparison of cranidia of *A. Chelonia impudens*, B, *Trochilopt. monochelone*, C, N.H.M. PR. 29, and C, *Chelonia*.
 ELLIOTT. *for. basis trabeculi basalis* and *basis trabeculi basalis*.



EXPLANATION OF PLATE 12

Dorsal and ventral views of skull and mandible of *Toxochelys latiremis* (A.M.N.H. 5118), the best-preserved skull known to date. One of hyoid elements lies across pterygoids. Nasal bones not visible.

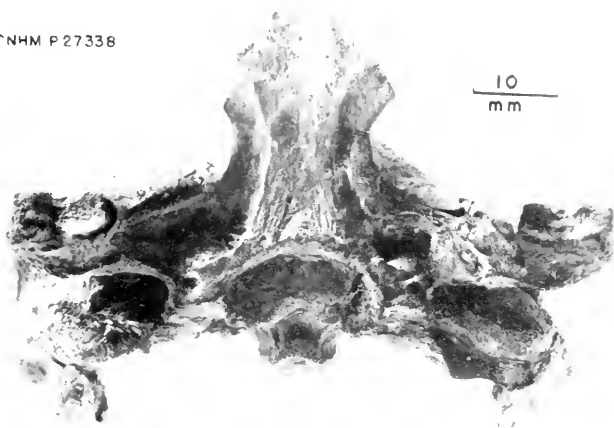




Skulls and mandibles of *Toxochelys latiremis* in dorsal and ventral view. Upper row, Y.P.M. 3604; middle row, A.M.N.H. 1497; lower row, Y.P.M. 3609.

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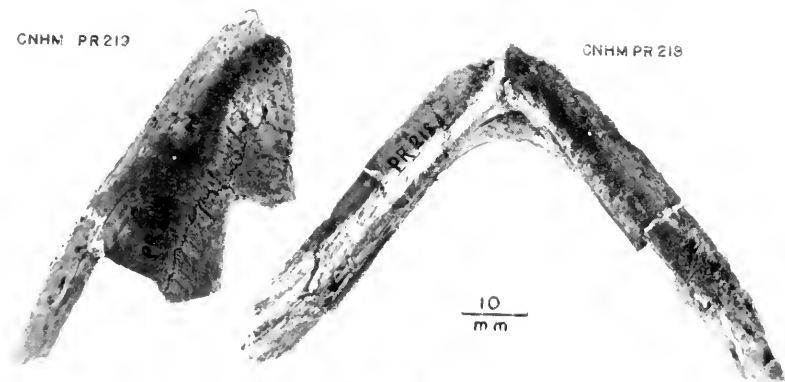
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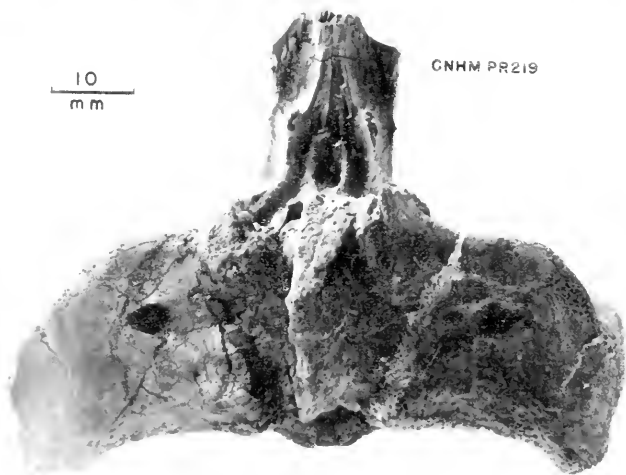
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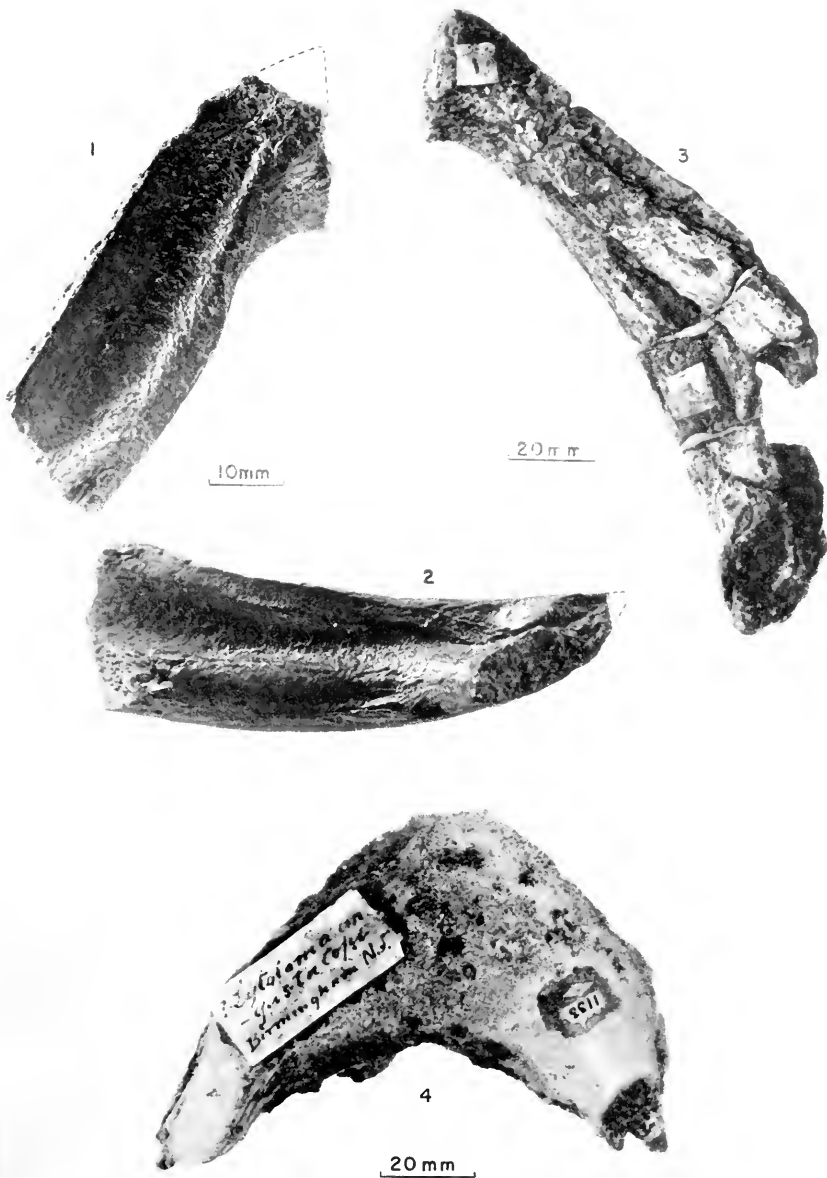
Skulls and mandibles of *Torochelys moorevillensis*.

EXPLANATION OF PLATE 15

Figs. 1 and 2. Dorsal and medial views of lower jaw (Y.P.M. 728) tentatively referred to *Torochelys atlantica*.

Fig. 3. Dorsal view of type specimen of *Torochelys latiremis*. Photograph by courtesy of American Museum of Natural History.

Fig. 4. Poorly preserved jaw fragment of *Osteopygis emarginatus* (A.M.N.H. 1133). This specimen is not the type of *Lytoloma angusta*; note question mark on label in Cope's handwriting. Photograph by courtesy of American Museum of Natural History.



EXPLANATION OF PLATE 16

Fig. 1. Dorsal views of mandibles of *Osteopygis emarginatus*: 1a, Y.P.M. 913; 1b, A.M. N.H. 2216; 1c, Y.P.M. 490; 1d, Y.P.M. 1001.

Fig. 2. Fragments of mandible of *Torochelys latiremis* (A.M.N.H. 1835, type of *Toxochelys serrifer*): 2a and 2b, dorsal and ventral views (uncrushed).

Figs. 3 and 8. Anterior and posterior views of quadrate of *Torochelys latiremis* (A.M. N.H. 1835).

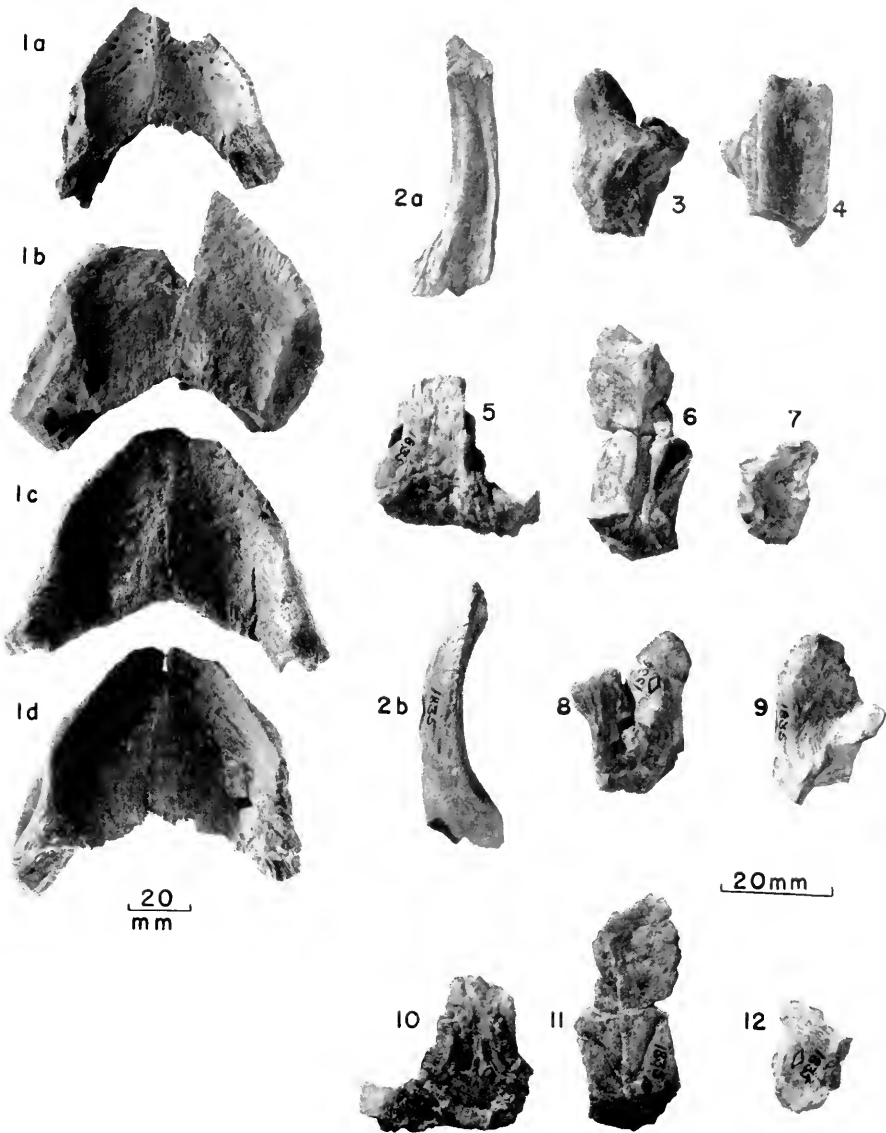
Figs. 4 and 9. Ventral and dorsal views of maxilla of *Torochelys latiremis* (A.M. N.H. 1835).

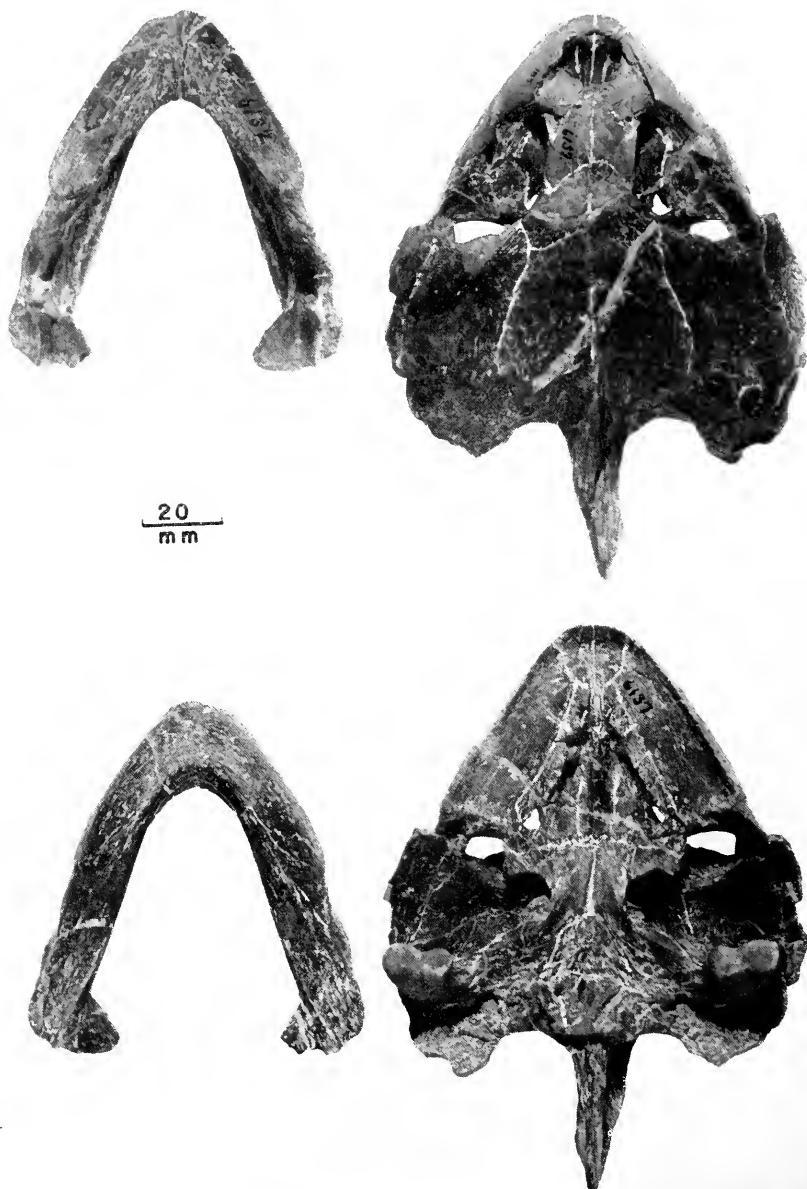
Figs. 5 and 10. Ventral and dorsal views of base of braincase of *Torochelys latiremis* (A.M.N.H. 1835).

Figs. 6 and 11. Ventral and dorsal views of parietal-frontal area of skull of *Torochelys latiremis* (A.M.N.H. 1835).

Figs. 7 and 12. Not definitely identifiable skull fragment.

Photograph by courtesy of American Museum of Natural History.

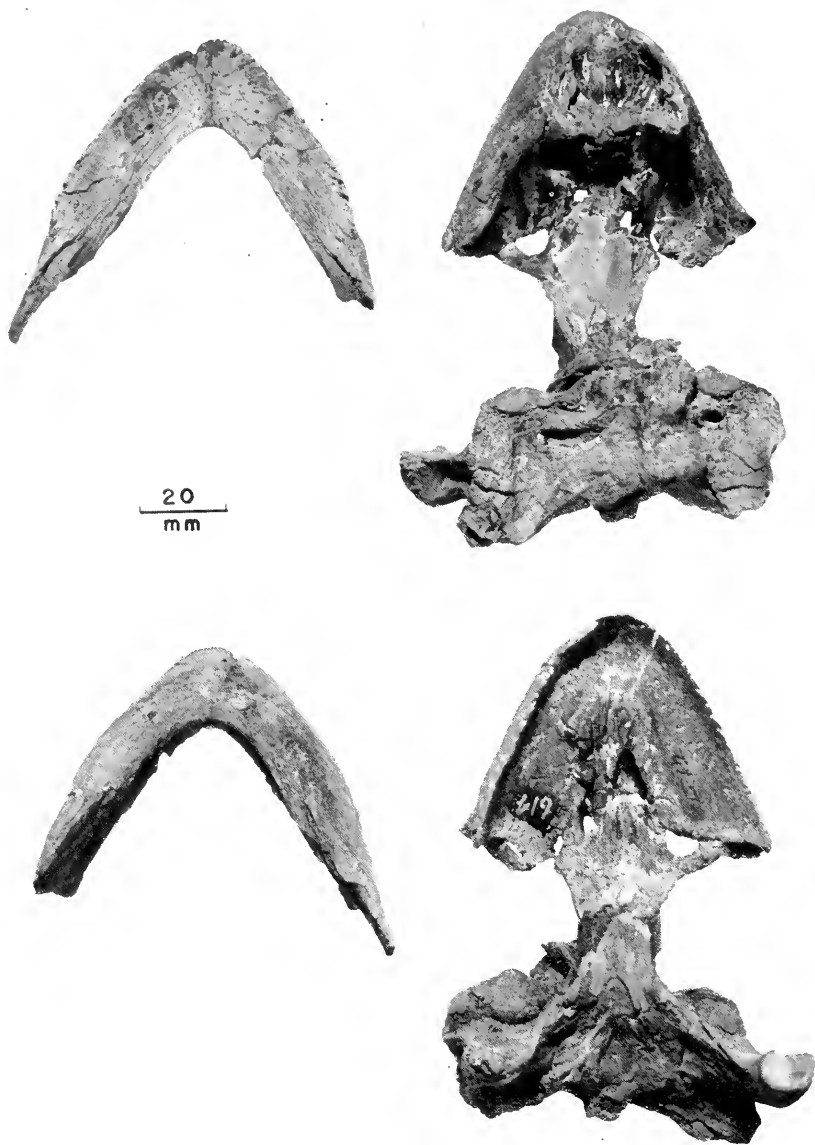




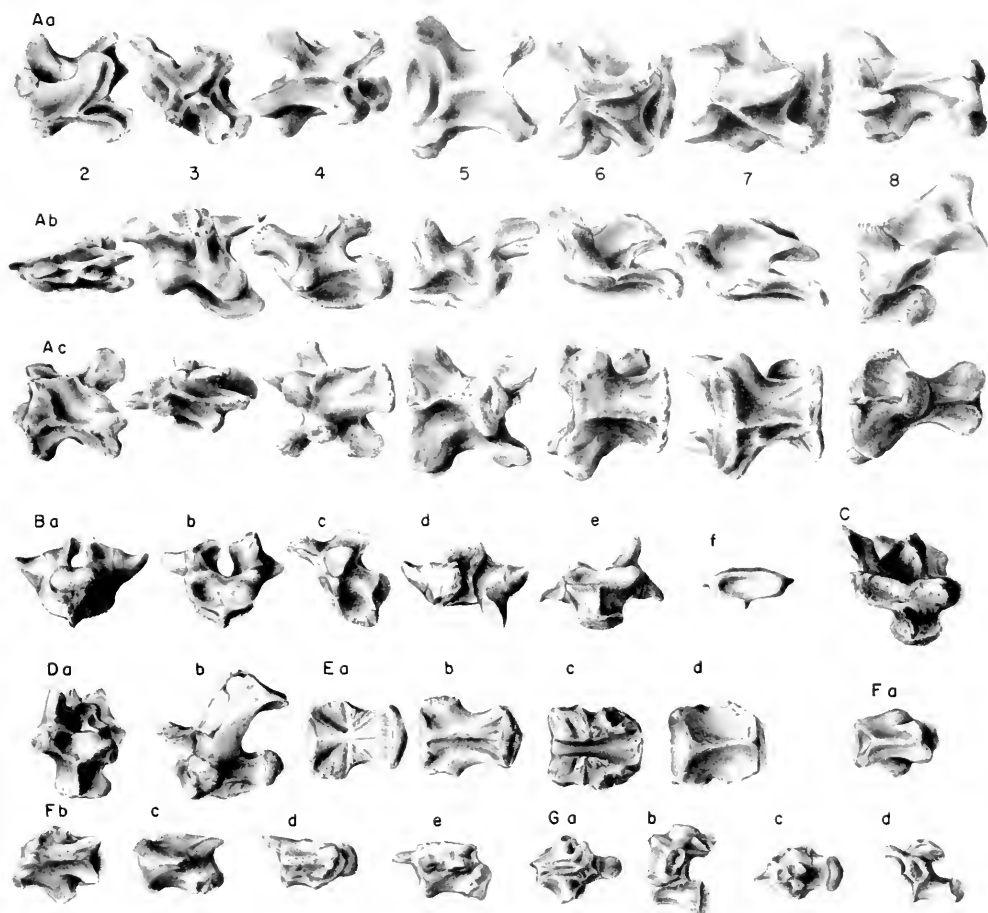
Ctenochelys stenopora (A.M.N.H. 6137, type of *Toxochelys elkader*). Skull and mandible in dorsal and ventral views.



Ctenochelys acris (C.N.H.M. P27337). Skull fragments and mandible, dorsal and ventral views.



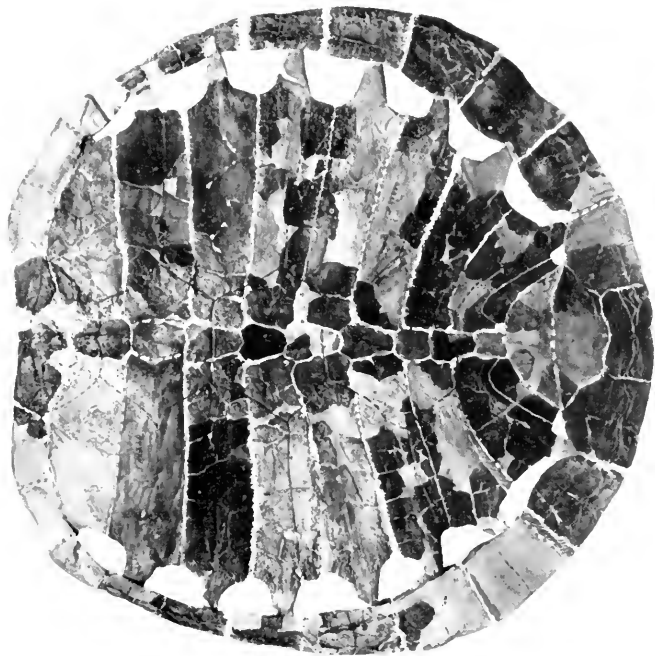
Ctenochelys procax (C.N.H.M. UC614). Skull and mandible in dorsal and ventral views.



Vertebrae of toxochelyid turtles. A, cervical vertebrae 2 to 8 of *Toxochelys latiremis* (C.N.H.M. PR123): Aa, in dorsal view; Ab, in side view; Ac, in ventral view. B, cervical vertebrae of *Toxochelys moorevillensis* (C.N.H.M. P27391): Ba, posterior, Bb, anterior, Bc, lateral, Bd, dorsal, Be, ventral views of eighth cervical vertebra (note the ribs); Bf, centrum of seventh cervical vertebra in anterior view. C, eighth cervical vertebra of *Toxochelys latiremis* (C.N.H.M. PR123) in anterior view. Da and Db, antero-ventral and lateral views of eighth cervical vertebra of *Ctenochelys acris*. Ea and Eb, dorsal and ventral views of centrum of sixth cervical vertebra, and Ec and Ed, dorsal and ventral views of centrum of first shell vertebra of *Ctenochelys tenuitesta* (C.N.H.M. P27361). F, *Ctenochelys acris* (C.N.H.M. P27352), caudal vertebrae: Fa, caudal vertebra in dorsal view; Fb and Fc, dorsal and lateral views of another caudal; Fd and Fe, dorsal and lateral views of a third, more posterior caudal vertebra. G, *Toxochelys moorevillensis* (C.N.H.M. P27391): Ga and Gb, posterior shell vertebra in dorsal and lateral view; Gc and Gd, ?second sacral vertebra in dorsal and lateral aspect.

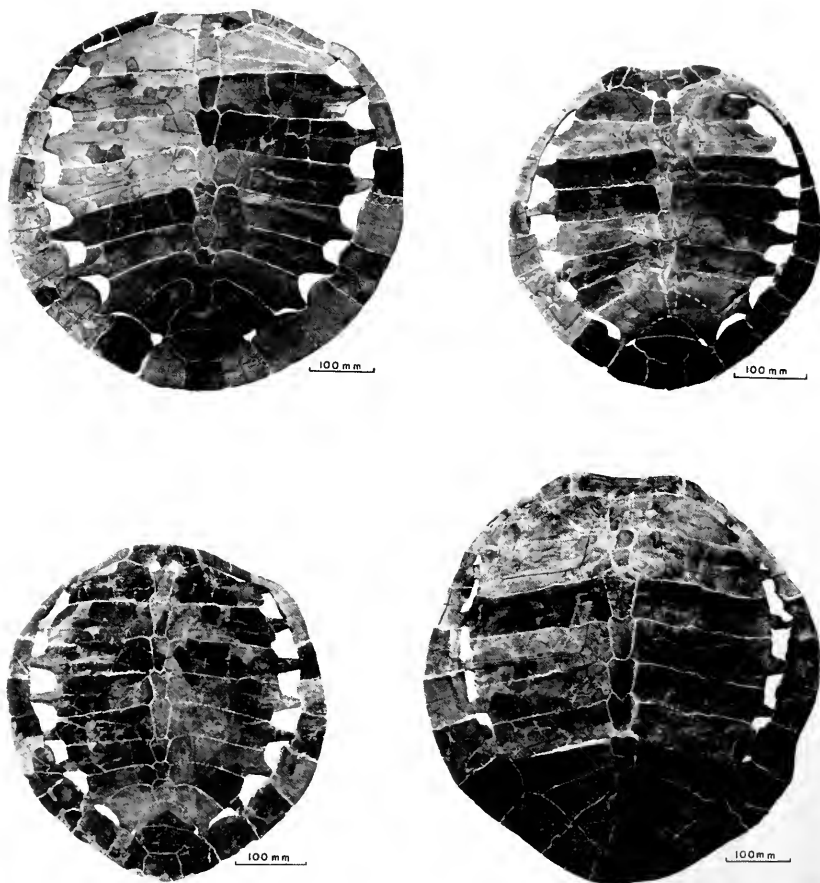


Juvenile specimen of *Torochelys latiremis*, K.U.(V.P.) 1244.

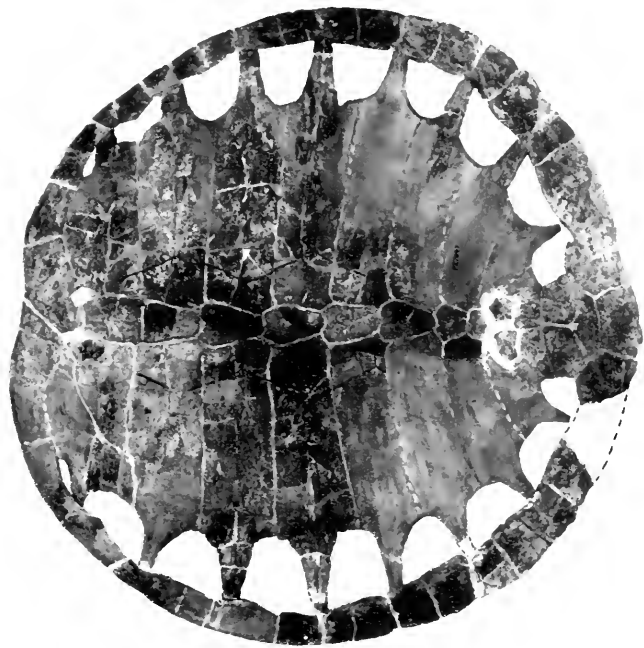


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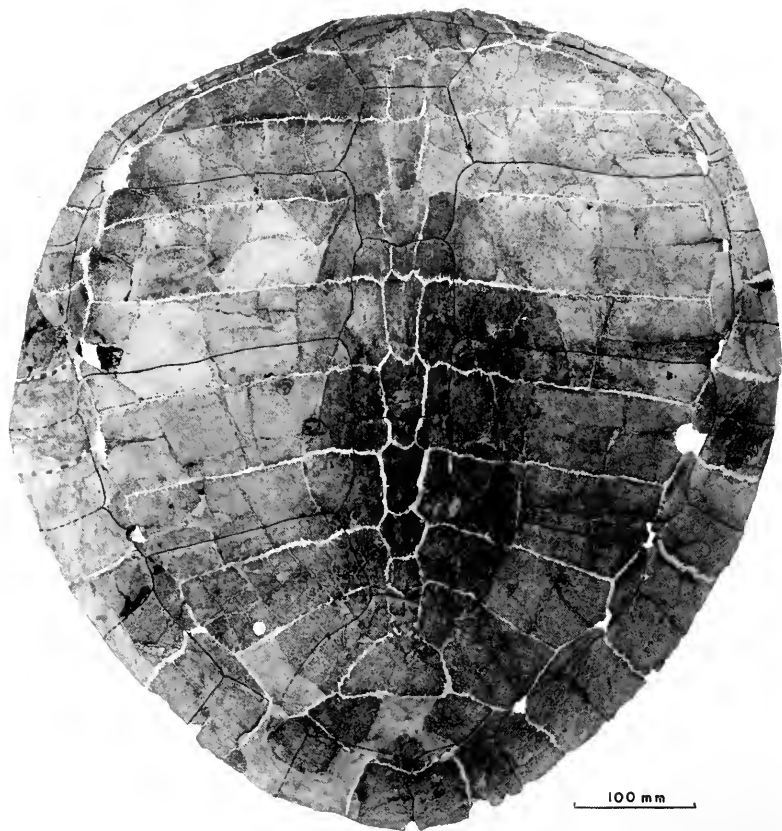
Carapace and plastron of *Torocheilus moorevillensis* (C.N.H.M. P27330).



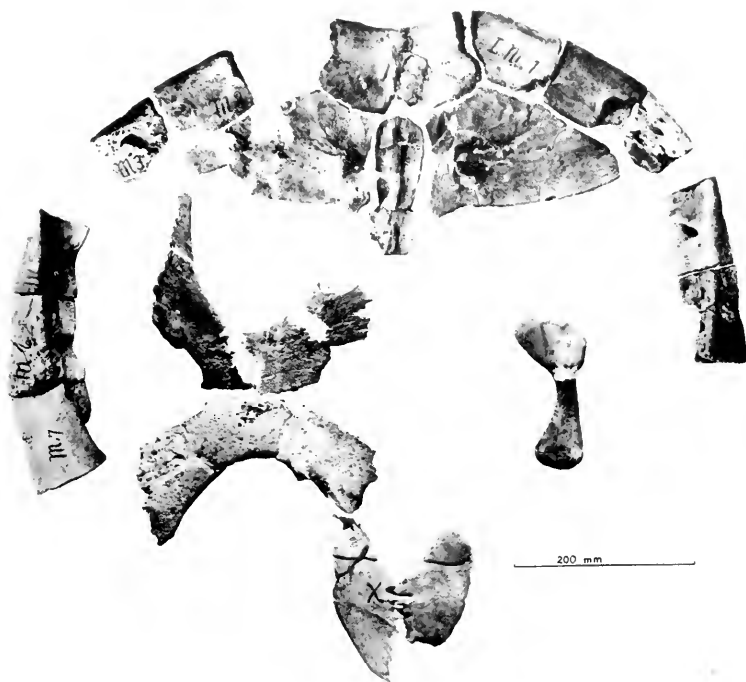
Carapace of *Toxochelys moorevillensis*. Upper left C.N.H.M. P27391, upper right C.N.H.M. PR167, lower left C.N.H.M. PR28, lower right C.N.H.M. PR136.



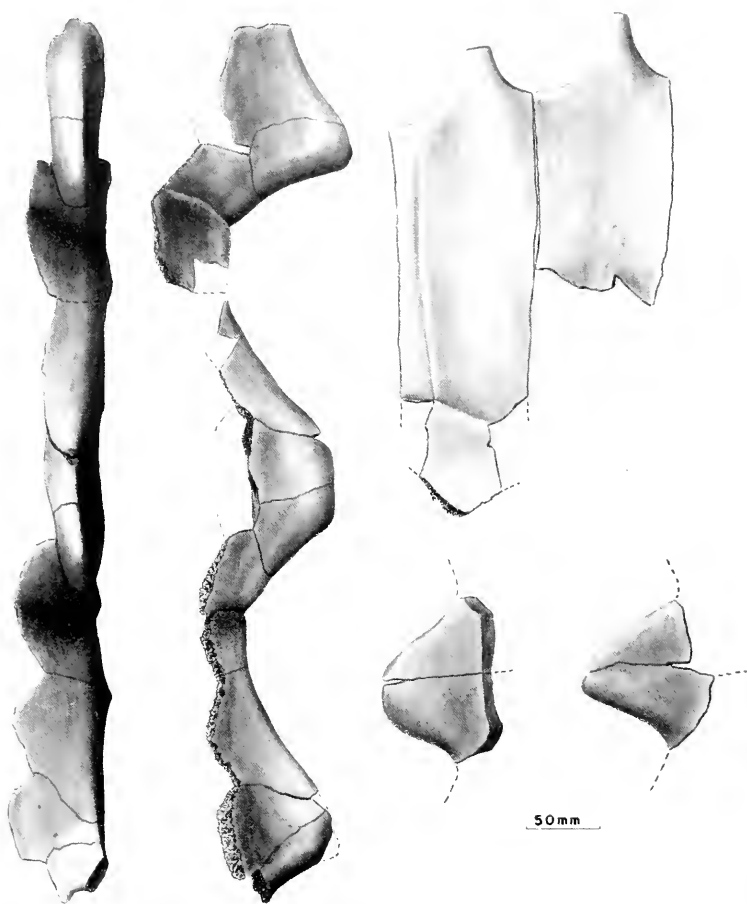
Carapace and plastron of *Torocheletys barberi* (C.N.H.M. P27047, type specimen).



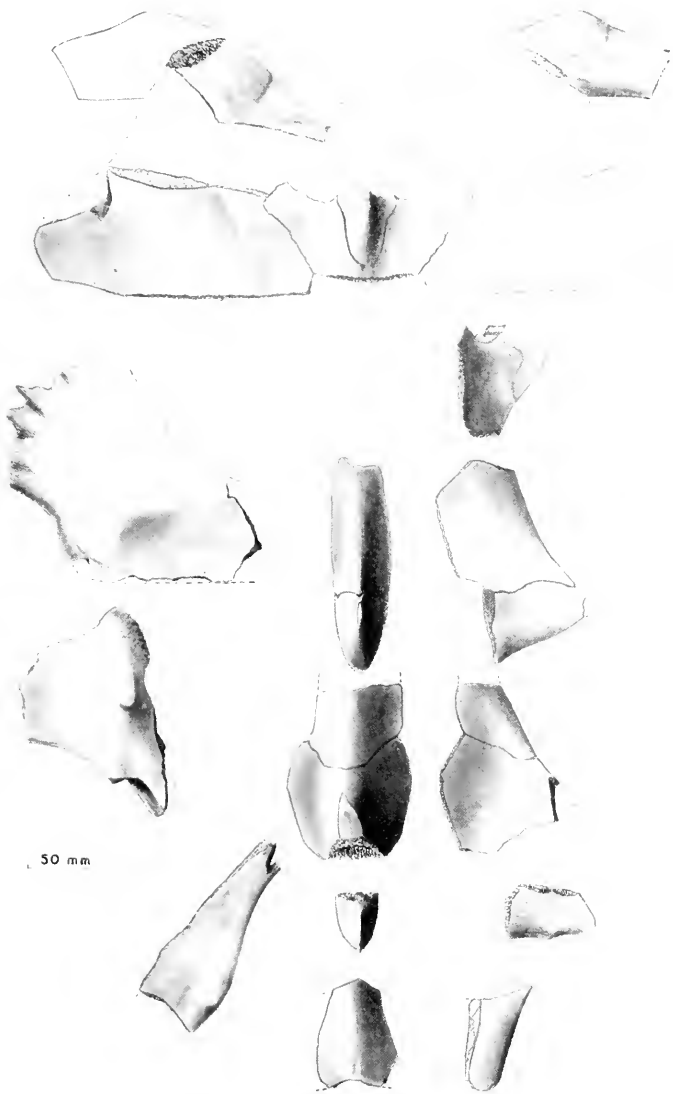
Carapace of *Thinochelys lapisossea* (C.N.H.M. P27453).



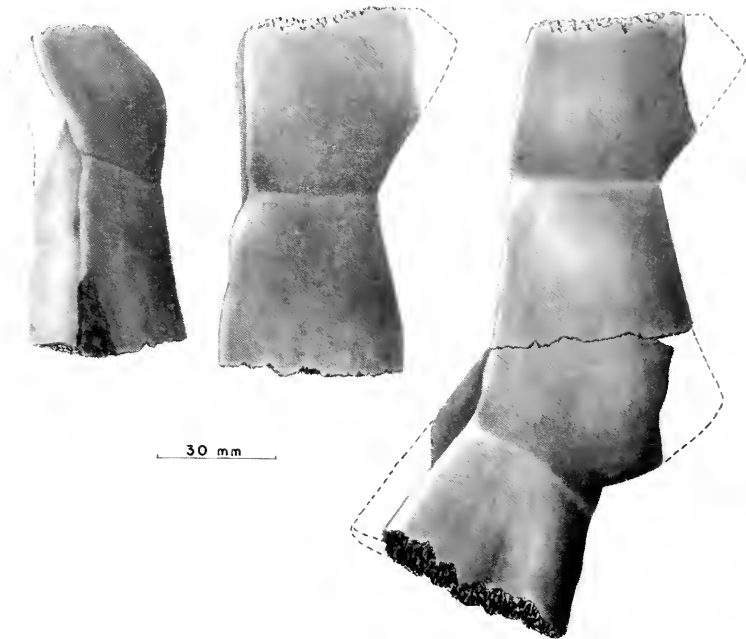
Carapace and plastron of *Osteopygis emarginatus* (Y.P.M. 778). Carapace in ventral view.



Prionocheilus nauta (C.N.H.M. P26237). Neural carina in dorsal and side views, two costal plates, and portions of peripheral plates.



Parts of carapace and plastron of *Prionochelys nauta* (C.N.H.M. P26238).



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Peripheral plates of *Prionochelys nauta* (C.N.H.M. P27456).

